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THE EFFECT OF FOOD ON GROWTH AND COLORATION OF THE TOPSHELL (*TURBO CORNUTUS* SOLANDER)[1]

By

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The topshell (*Turbo cornutus* Solander) is a common herbivorous marine gastropod, distributed in areas of the warm coastal current of Japan. It is a valuable food item and therefore of commercial importance. Under natural conditions the shell is highly spinous and the color greenish brown.

In a previous paper (Ino, 1943) it was reported that the spines did not develop when the mollusk was transported from its normal environment into a calm, dark habitat, and that under these conditions the shell color changed to whitish. The food in this dark habitat consisted of only brown algae, *Eisenia bicyclis*. In order to determine whether absence of light or a changed diet was responsible for the physical change in the color of the shell, studies were performed with a carefully regulated diet and with certain individuals blinded.

MATERIAL AND METHOD

The topshells selected for the experiment were divided into two groups: Group 1 animals were fed a normal diet consisting of *Eisenia bicyclis* (Plate IA) plus calcareous algae (*Cheilosporum maximum*

[1] Contribution from the Kominato Marine Biological Laboratory of the Tokyo College of Fisheries (No. 12).

[2] I wish to acknowledge the assistance of Mr. Noboru Noju, who gave valuable help during this work.

(Plate IB) and *Corallina pilulifera*), while Group 2 animals received *Eisenia bicyclis* only. The mollusks used were placed in bamboo baskets and fed abundantly on their respective diets, the baskets being kept in an artificial pool filled with sea water (Fig. 1). These experimental conditions established a habitat that was both calmer and darker than that of the normal environment, with the temperature and salinity slightly lower than that encountered by the animals under natural conditions.

The experiment was begun on April 15, 1943 and concluded on October 3, 1943, when an exceptionally severe storm wrecked the pond. In the beginning each basket contained twelve individuals, six of

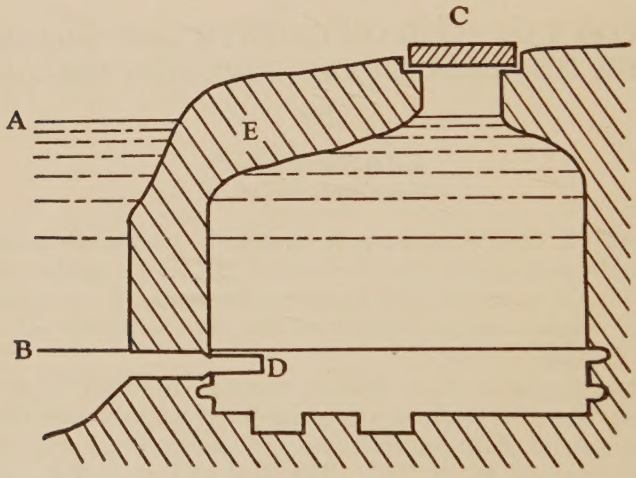

Figure 1. Longitudinal section of the experimental pond. A—High water mark. B—Low water mark. C—Lid. D—Gateway of sea water. E—Rock.

which had been blinded by an operation that consisted of amputating the eye stalk. To perform this operation it was necessary to break the outer lip of the shell aperture sufficiently so that the animal could not conceal its head within the shell. The operation proved to be too severe and six of the operated animals died within twenty days. Three individuals, two operated and one with normal vision, were washed away by the storm that terminated the experiment. In the final analysis, the number of animals was reduced to seven individuals in Group 1 and eight individuals in Group 2. This number, however, proved sufficient to yield definite results.

RESULTS

The following results were noted on the 15 surviving individuals:

Growth and Change of Spines on the Shell. The shell length of individuals growing under normal food conditions (Group 1) showed an average increase in length of 19% during the course of the experiment, whereas individuals fed *Eisenia* alone (Group 2) showed an average increase in length of 14% (Table I). It was noted that normal spines

TABLE I.—Increase in Size of Shell and Weight of *Turbo cornutus* under Controlled Feeding Conditions from April 15 to October 3, 1943

Food	Eyes	No.	Shell length (cm.)				Weight (g.)			
			IV/15	VI/3	VII/3	X/3	IV1/5	VI/3	VII/3	X/3
Group 1 *Eisenia* plus calcareous algae	Blind	986	4.06	4.33	4.49	5.18	17.2	19.4	21.3	?
		998	3.71	3.71	3.82	4.54	13.1	13.7	16.0	?
	Normal	989	4.75	4.92	5.02	5.50	24.5	28.4	33.0	?
		979	4.45	4.62	4.78	5.19	23.2	25.4	27.3	?
		968	4.20	4.32	4.45	5.10	17.7	21.7	23.6	?
		999	4.07	4.15	4.22	4.86	16.5	18.4	19.5	?
		977	3.58	3.58	3.58	3.85	12.7	13.5	13.7	?
Mean			4.11	4.23	4.33	4.89	17.8	20.1	22.1	?
Group 2 *Eisenia*	Blind	983	3.63	3.65	3.80	4.45	13.3	13.5	14.5	?
		992	3.51	3.55	3.80	4.35	12.4	13.2	14.4	?
	Normal	971	5.24	5.24	5.29	5.38	34.2	36.4	37.9	?
		991	4.85	4.98	5.10	5.45	29.9	32.2	35.6	?
		975	4.60	4.70	4.80	5.22	21.9	24.9	26.9	?
		980	4.52	4.63	4.82	5.20	23.4	26.2	29.2	?
		987	4.35	4.42	4.58	4.92	19.7	21.8	23.5	?
		988	3.95	4.10	4.25	4.64	15.4	17.3	19.5	?
Mean			4.33	4.41	4.56	4.95	21.3	23.2	25.2	?

did not develop on the portion of the shell generated during the period of the experiment, although a few weak spines were present on certain individuals in both groups of shells (Table II). This suppression of

TABLE II.—Increase in Number of Spines of *Turbo cornutus* under Controlled Feeding Conditions

Spines		Group 1 (*Food: Eisenia plus calcareous algae*)							Group 2 (*Food: Eisenia*)						
		Blind		Normal					Blind		Normal				
		986	998	989	979	968	999	977	983	992	971	991	975	980	987	988
A*	Upper row	0	0	6	6	7	2	8	0	0	10	7	9	5	3	5
	Lower row	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B†	Upper row	0	0	1	0	1	0	2	0	0	0	0	0	3	0	1
	Lower row	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0

* Number of spines before controlled feeding.

† Newly developed number after controlled feeding.

spine growth was discussed in a previous paper (Ino, 1943) and was probably due to changed factors caused by removal from the natural environment to a closed tank where temperature and salinity were lower.

Color Changes in the Shell. *Turbo cornutus* fed with *Eisenia* plus calcareous algae did not show any marked color change in the newly formed parts of the shell (Plate II, Table III). A color change was

TABLE III.—Color Changes in Shell of *Turbo cornutus* under Controlled Feeding

	Group 1 — Food: *Eisenia* plus calcareous algae							Group 2 — Food: *Eisenia*							
	986	*998*	*989*	*979*	*968*	*999*	*977*	*983*	*992*	*971*	*991*	*975*	*980*	*987*	*988*
Color* of shell before experiment	B	B	B	B	B	B	B	B	G	G	B	B	G	B	B
	P	P	P	P	P	G	P	P	P	B	P	P	B	P	P
	W	G	G	G	G	P	G	G	W	P	G	G	P	G	G
	G	W	W	W	W	W	W	W	B		W	W	W	W	W
Color* of newly formed area after experiment	P	W	P	B	B	B	W								
	W	B	B	W	W	W	B	W	W	W	W	W	W	W	W
	B	P	W	P	P	P	P								
	G	G	G	G	G	G	G								

* Colors on each shell are listed in order of intensity as determined by visual inspection. B—Brown; P—Purple; W—White; and G—Green.

apparent when the food consisted of *Eisenia* alone. The appearance of the newly grown part of the shell was white, with almost no trace of color (Plate III, Table III). Blinded top shells in this group also showed this color change. It is concluded, therefore, that the color change resulted from the change in diet.

DISCUSSION

This study yielded the same results as shown previously (Ino, 1943) relative to spine development and change of shell color in the topshell. Now, however, it can be stated definitely that the type of algal food influences shell color. Many students have pointed out the presence of calcareous algae in the alimentary tract of these mollusks, but it was generally assumed that these plants were picked up incidentally while the topshells were searching for food. It is now concluded that calcareous algae are important foods for this species under natural conditions.

Colton (1916) noted that the shell color of *Purpura lapillus* was influenced by the environment. In the same species, Moore (1936) reported the close correlation of color (brown or mauve) with the abundance of *Mytilus* in the diet. Various other authors have described color variation in relation to environment, but Moore's work

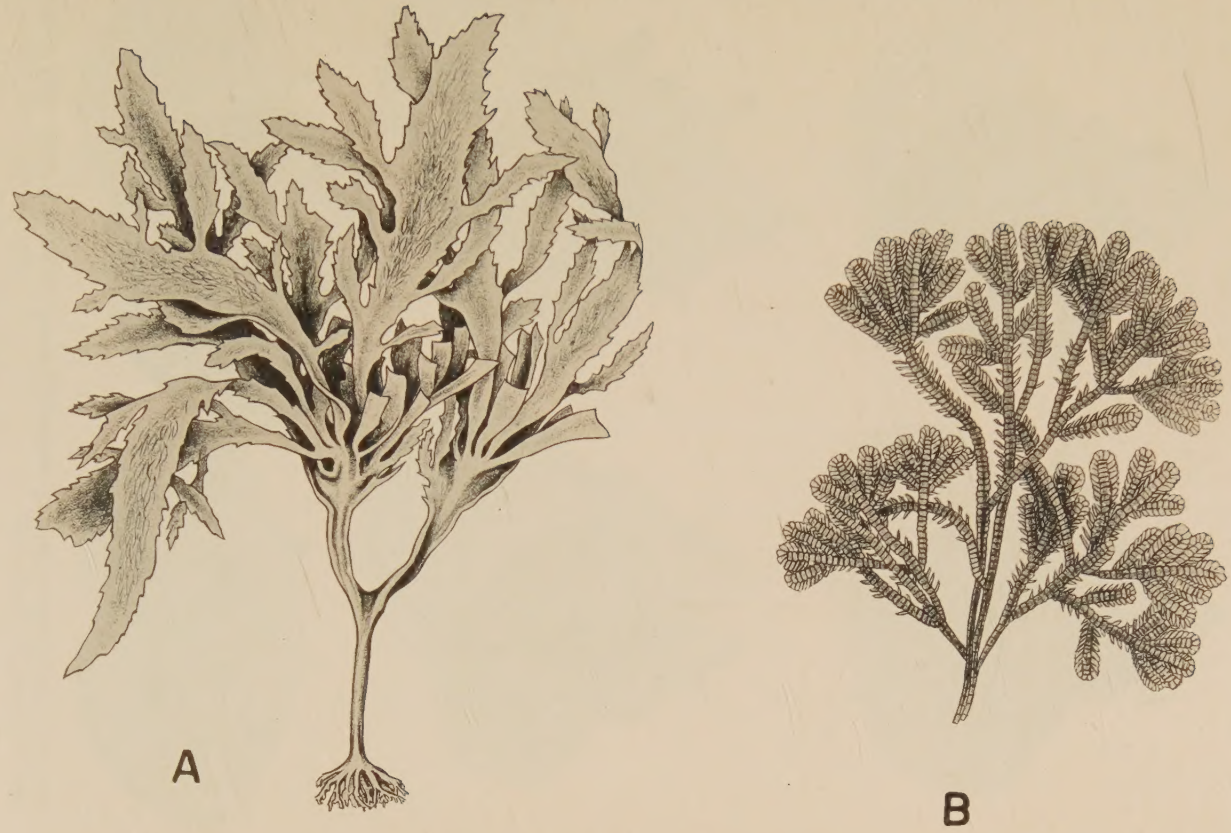

Plate I. A. *Eisenia bicyclis*. B. *Cheilosporum maximum*.

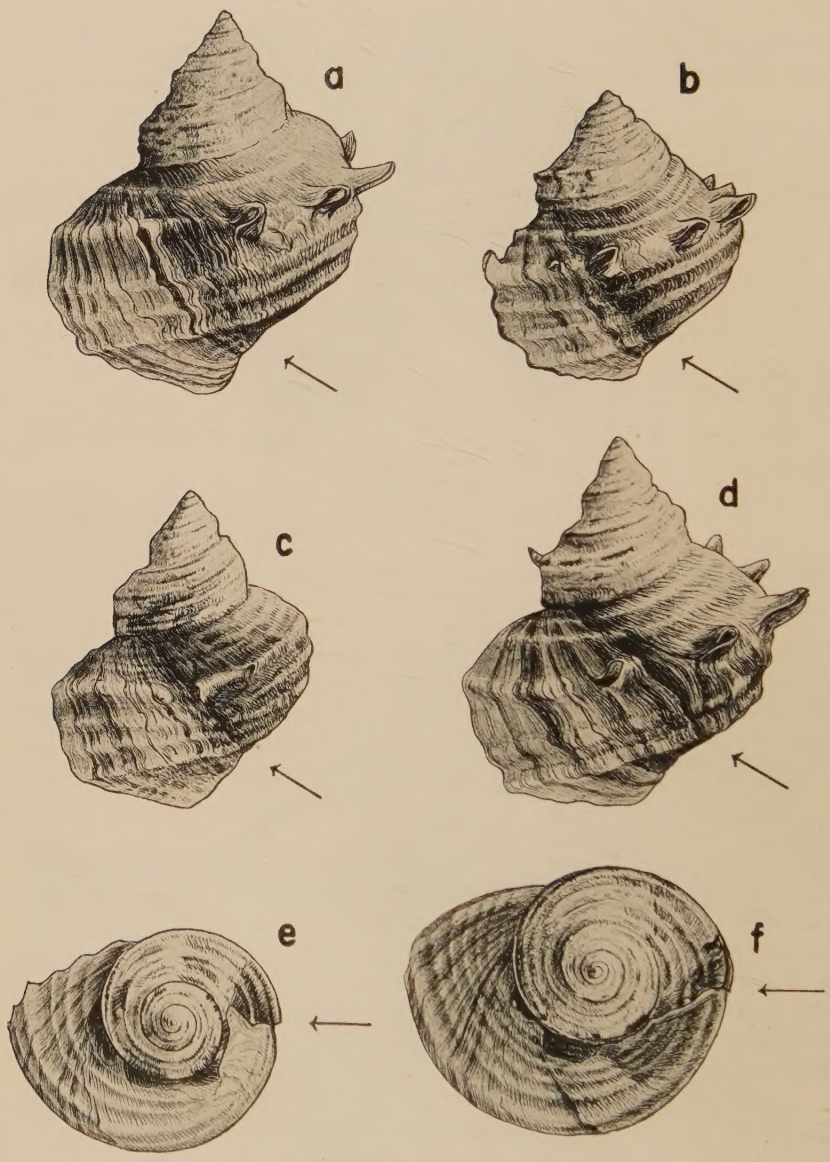

Plate II. *Turbo cornutus* (Group 1). Normal individuals: a – 979; b – 977; c – 999; d – 989. Blind individuals: e – 998; f – 986.

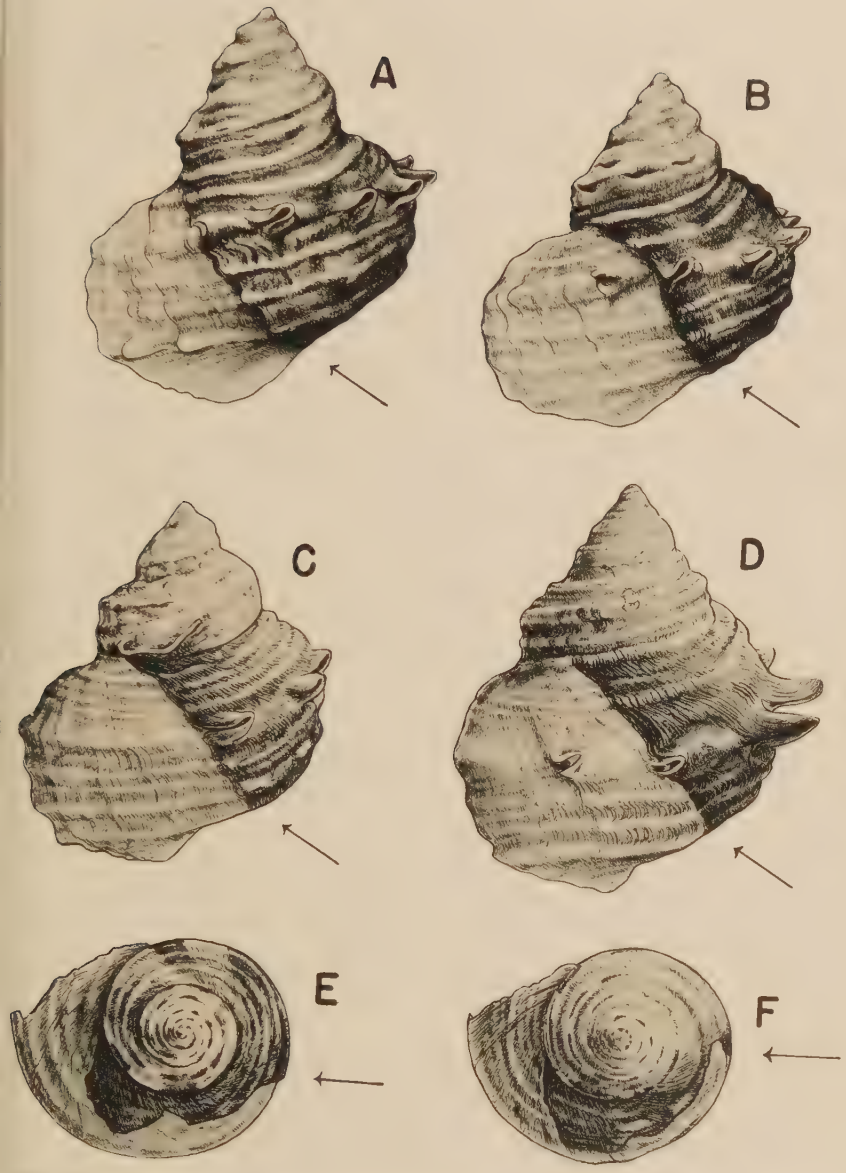

Plate III. *Turbo cornutus* (Group 2). Normal individuals: A – 975; B – 988; C – 987; D – 991. Blind individuals: E – 983; F – 992.

was the first report in which the influence of diet on shell color had been indicated. However, *Purpura* is a carnivorous gastropod as opposed to the herbivorous *Turbo*. The shell is produced by the mantle edge. Therefore, the physiological mechanism by means of which the color pigment is controlled and then transported to the mantle edge is an interesting problem for future study.

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1943. Feeding intensity and change of the shell of the topshell (*Turbo cornutus* Solander) due to environments. Bull. Jap. Soc. sci. Fish., *12* (3): 113–118.

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THE DIATOMS COLLECTED BY THE U. S. S. CACOPAN IN THE ANTARCTIC IN 1947[1]

By

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For investigation of the Diatomaceae, a series of water samples was collected from the U. S. S. CACOPAN by filling a citrate bottle either with surface water obtained with a bucket or with water obtained from various depths with Nansen bottles. The positions at which samples were collected in the Antarctic are plotted on Fig. 1. Of the main previous Antarctic Expeditions (CHALLENGER, DEUTSCHER SUDPOLAR, VALDIVIA and DISCOVERY) only the CHALLENGER collected much diatom material on the Pacific and Indian Ocean side of the Antarctic continent. Five stations were occupied by the CHALLENGER in this area, but most of the diatom material obtained was from bottom sediments. The species of diatoms found at each station by the CACOPAN are listed in Table I with notations indicating the relative abundance of diatoms at each station. Further information on each station (Depth, Temperature, etc.) is given in the APPENDIX.

Identification and estimation of abundance were carried out on semi-permanent strewn plankton mounts. The diatoms were washed six times in distilled water, allowed to settle for 24 hours between washings, and the supernatant water drawn off by means of a fine pipette attached to a vacuum pump. After the final washing a few drops of the sediment were placed on a slide, gently warmed until dry, and a permanent mount prepared. For a critical examination of the species a mountant with a high refractive index is necessary. For this purpose Hyrax (a synthetic resin with a refractive index of 1.71) was used. These preparations give excellent results and last for many months.

According to the hydrographic data (Pritchard and LaFond, MS.), the Antarctic Convergence is not sharply defined in the region from which most of the diatom samples were taken, but lies somewhere between Lat. 59° S. and 63° S. The surface water temperature difference—about 6° C.—between stations 42 and 44 is an indication that the Convergence had been crossed, and all higher numbered stations were therefore situated to the north of the Convergence. It appears

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 416.

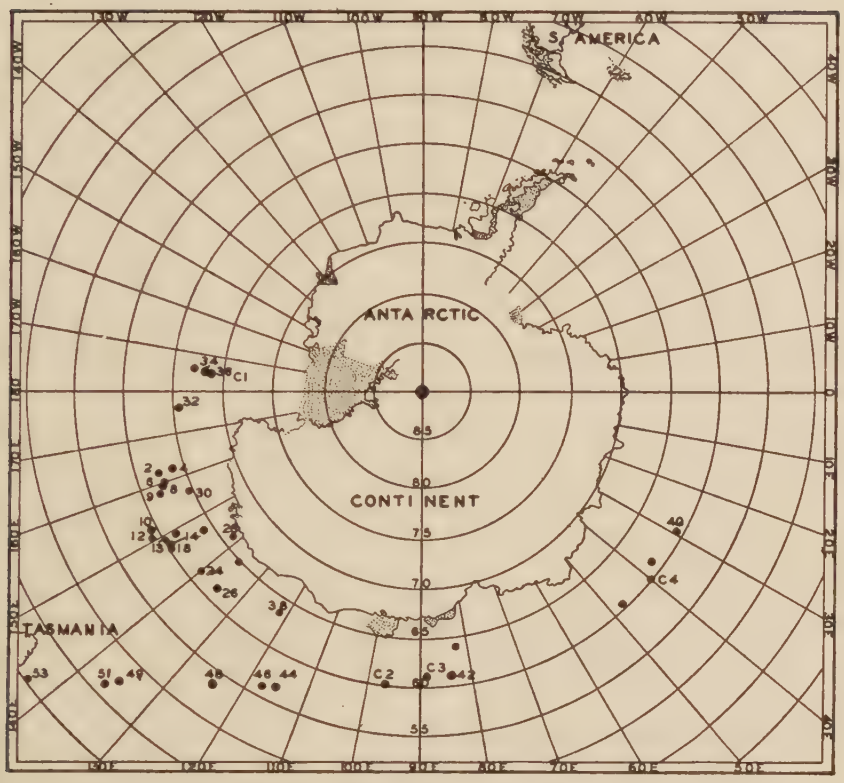
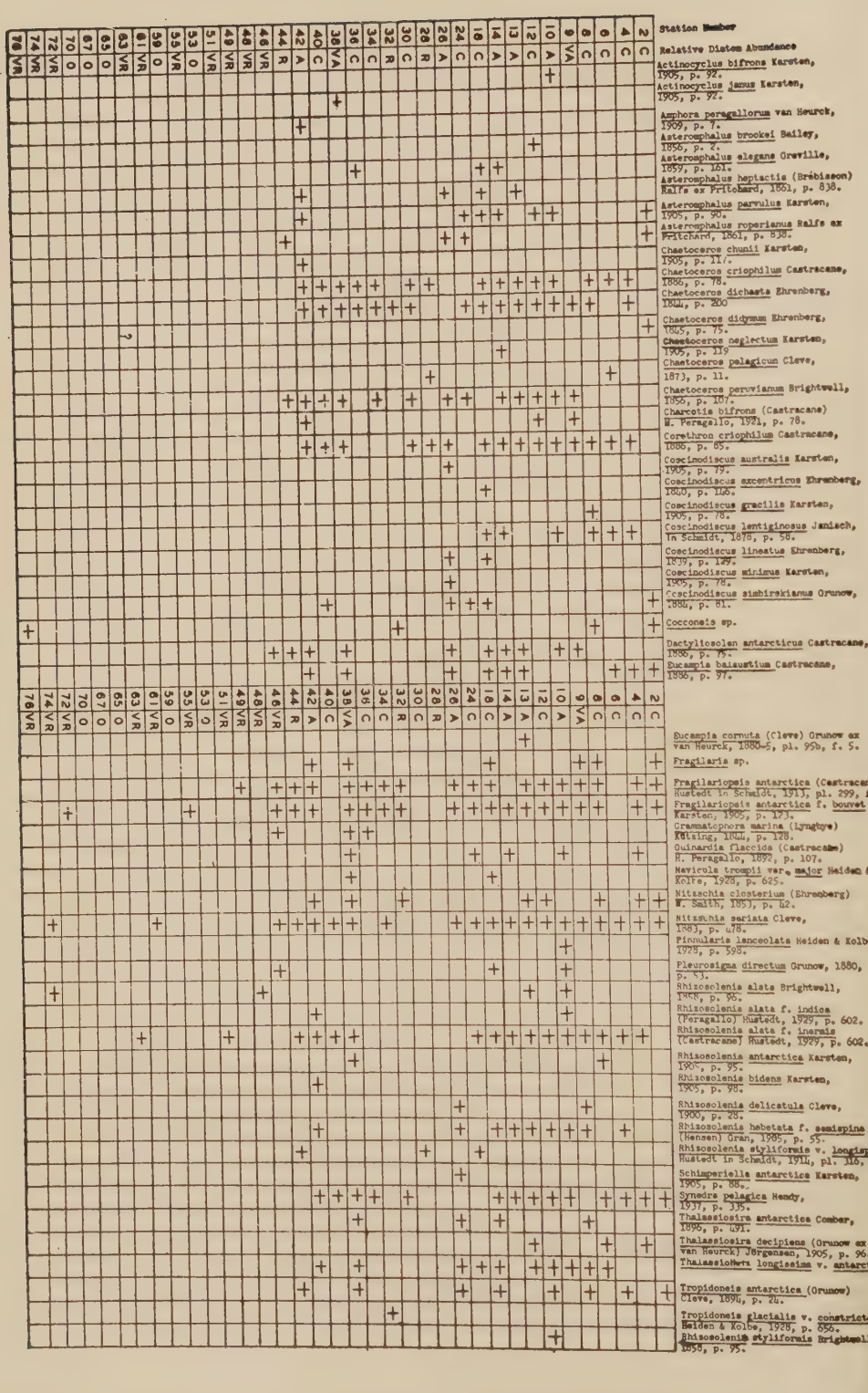


Figure 1. Chart of Antarctic stations.

from Table I that the Antarctic Circumpolar surface water south of the Convergence supports an extremely rich phytoplankton population compared with the striking paucity of phytoplankton in the surface waters to the north of the Convergence. The phytoplankton wealth of the Antarctic waters has frequently been commented upon before (Hendey, 1937; Hart, 1934). Hart has suggested that the diminished population in the subtropical and tropical regions is a result of the almost complete lack of nutrient salts in the surface waters of these regions, while in the polar regions nutrients cannot be regarded as a limiting factor at any time, since the content never falls below a minimum of about 0.9 μg.-at. PO_4 per liter, which is well above diatom needs. Hart considers that the high nutrient content is due to the fact that the spring break-up of the ice packs releases a supply that is never exhausted. Another cause of this nutrient surplus, and probably the main cause, is the marked vertical mixing of the Antarctic waters


Station Number
Relative Diatom Abundance
Actinocyclus bifrons Karsten, 1905, p. 92.
Actinocyclus janus Karsten, 1905, p. 92.
Amphora peragallorum van Heurck, 1909, p. 7.
Asteromphalus brookei Bailey, 1856, p. 4.
Asteromphalus elegans Greville, 1859, p. 161.
Asteromphalus heptactis (Brébisson) Ralfs ex Pritchard, 1861, p. 838.
Asteromphalus parvulus Karsten, 1905, p. 90.
Asteromphalus roperianus Ralfs ex Pritchard, 1861, p. 838.
Chaetoceros chunii Karsten, 1905, p. 117.
Chaetoceros criophilus Castracane, 1886, p. 78.
Chaetoceros dichaeta Ehrenberg, 1841, p. 200
Chaetoceros didymus Ehrenberg, 1845, p. 75.
Chaetoceros neglectus Karsten, 1905, p. 119
Chaetoceros pelagicus Cleve, 1873, p. 11.
Chaetoceros peruvianus Brightwell, 1856, p. 107.
Charcotia bifrons (Castracane) H. Peragallo, 1921, p. 78.
Corethron criophilus Castracane, 1886, p. 85.
Coscinodiscus australis Karsten, 1905, p. 79.
Coscinodiscus excentricus Ehrenberg, 1840, p. 106.
Coscinodiscus gracilis Karsten, 1905, p. 78.
Coscinodiscus lentiginosus Janisch, in Schmidt, 1878, p. 58.
Coscinodiscus lineatus Ehrenberg, 1839, p. 129.
Coscinodiscus minimus Karsten, 1905, p. 78.
Coscinodiscus simbirskianus Grunow, 1884, p. 81.
Cocconeis sp.
Dactyliosolen antarcticus Castracane, 1886, p. 75.
Eucampia balaustium Castracane, 1886, p. 97.
Eucampia cornuta (Cleve) Grunow ex van Heurck, 1880-5, pl. 95b, f. 5.
Fragilaria sp.
Fragilariopsis antarctica (Castracane) Hustedt in Schmidt, 1913, pl. 299, f. 9-
Fragilariopsis antarctica f. bouvet Karsten, 1905, p. 123.
Grammatophora marina (Lyngbye) Kützing, 1844, p. 128.
Guinardia flaccida (Castracane) H. Peragallo, 1892, p. 107.
Navicula trompii var. major Heiden & Kolbe, 1928, p. 625.
Nitzschia closterium (Ehrenberg) W. Smith, 1853, p. 42.
Nitzschia seriata Cleve, 1883, p. 478.
Pinnularia lanceolata Heiden & Kolbe 1928, p. 593.
Pleurosigma directum Grunow, 1880, p. 51.
Rhizosolenia alata Brightwell, 1858, p. 96.
Rhizosolenia alata f. indica (Peragallo) Hustedt, 1929, p. 602.
Rhizosolenia alata f. inermis (Castracane) Hustedt, 1929, p. 602.
Rhizosolenia antarctica Karsten, 1905, p. 95.
Rhizosolenia bidens Karsten, 1905, p. 98.
Rhizosolenia delicatula Cleve, 1900, p. 28.
Rhizosolenia hebetata f. semispina (Hensen) Gran, 1905, p. 55.
Rhizosolenia styliformis v. longispina Hustedt in Schmidt, 1911, pl. 116, f 9
Schimperiella antarctica Karsten, 1905, p. 88.
Synedra pelagica Hendy, 1937, p. 135.
Thalassiosira antarctica Comber, 1896, p. 491.
Thalassiosira decipiens (Grunow ex van Heurck) Jörgensen, 1905, p. 96.
Thalassiothrix longissima v. antarctica
Tropidoneis antarctica (Grunow) Cleve, 1894, p. 24.
Tropidoneis glacialis v. constricta Heiden & Kolbe, 1928, p. 656.
Rhizosolenia styliformis Brightwell, 1858, p. 95.

and weak thermal stratification resulting in the ascent of nutrient-rich deep water (Sverdrup, Johnson and Fleming, 1942: 620). This nutrient surplus was also indicated by the CACOPAN collection.

Four hydrographic stations, shown in Fig. 1, were occupied in the polar waters. The vertical thermal structure at these four stations (Fig. 2) reveals a marked seasonal thermocline with a drop in temperature of nearly 5° C. at depths of 20–40 meters.[2] The presence of this stratification shows that the surface waters there have already spent some time as such. A certain degree of vertical stability, as is indicated here, has been considered necessary for maximum diatom production, otherwise many of the diatoms are carried down below the euphotic zone (Gran and Braarud, in Sverdrup, et al., 1942: 789). Thus, although data on the actual nutrient content of the water are lacking, the high diatom population in the euphotic zone above the thermocline (in surface waters which are "aged") is strong evidence that there is still a sufficiency of nutrients for good phytoplankton production.

On crossing the Antarctic Convergence to the north, a pronounced drop in phytoplankton population is noted. The thermal structure in this region (Fig. 3) can be taken as an indication that vertical movement between the waters of the euphotic zone above the thermocline and the lower layers is much reduced, and thus the replenishment of nutrients is slow. The paucity of diatom cells here may indicate that the vernal bloom is over and that the surface water nutrients are depleted. The appearance of a summer form such as *Rhizosolenia hebetata* f. *semispina* and the absence of the primitive resting stage of *Rhizosolenia hebetata* are indications that the population is a summer one.

The species concentration found at each depth at the hydrographic stations is as follows:

Station C1		*Station C2*		*Station C3*		*Station C4*	
Depth (feet)	*No. of Species*	*Depth (feet)*	*No. of Species*	*Depth (feet)*	*No. of Species*	*Depth (feet)*	*No. of Species*
0	3	0	1	0	8	0	3
50	1	50	7	50	9	50	8
100	1	100	7	100	6	100	8
200	1	200	1	200	5	200	8
300	0	300	2	300	1	300	0
500	0	500	1	600	0	500	0
900	0	900	1			650	0

As each species was usually represented by only one or two frustules, the number of species can be taken as an indication of diatom concen-

[2] There is no winter thermocline in Antarctic waters (Sverdrup, et al., 1942: 609).

Table I. Species and Abundance of Diatoms. VA—very abundant, A—abundant, C—common, R—rare, VR—very rare, O—None detected.

tration. The depths at which a Secchi disc could be seen at these four stations were as follows: Sta. C1, 90 ft.; Sta. C2, 55 ft.; Sta. C3, 41 ft.; Sta. C4, 68 ft. Diatoms flourish best in somewhat subdued

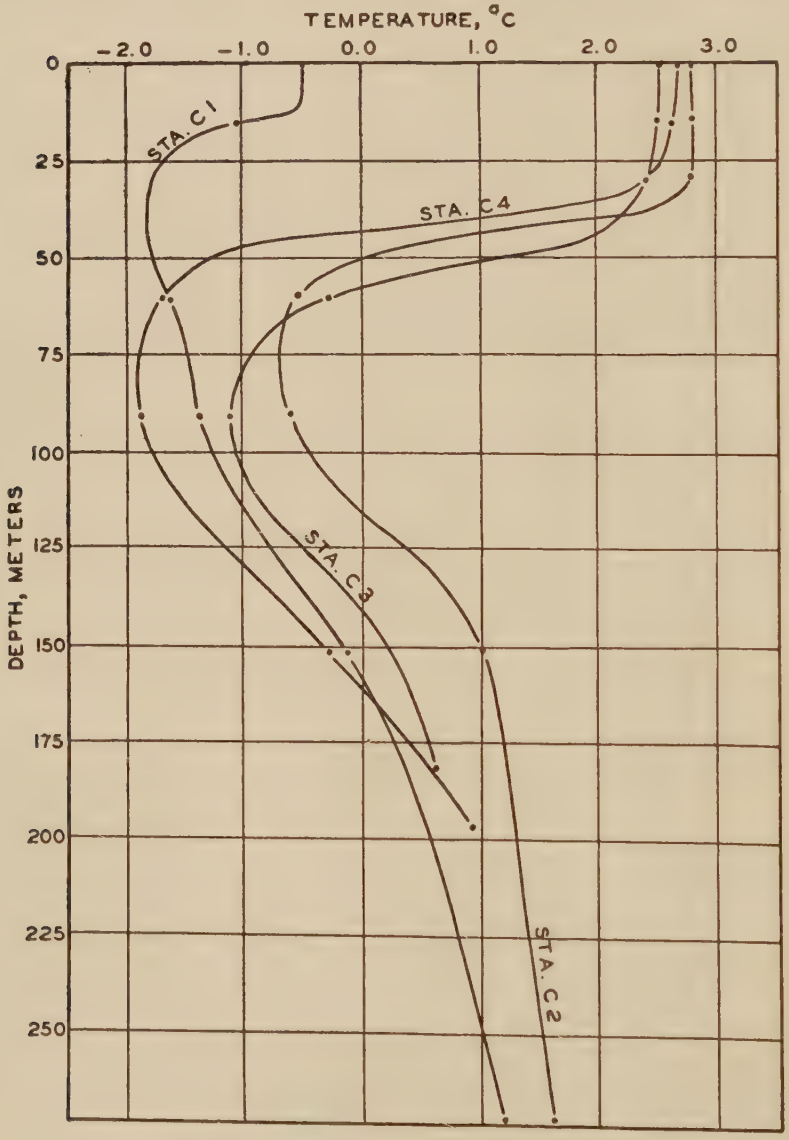


Figure 2. Vertical thermal structure at hydrographic stations.

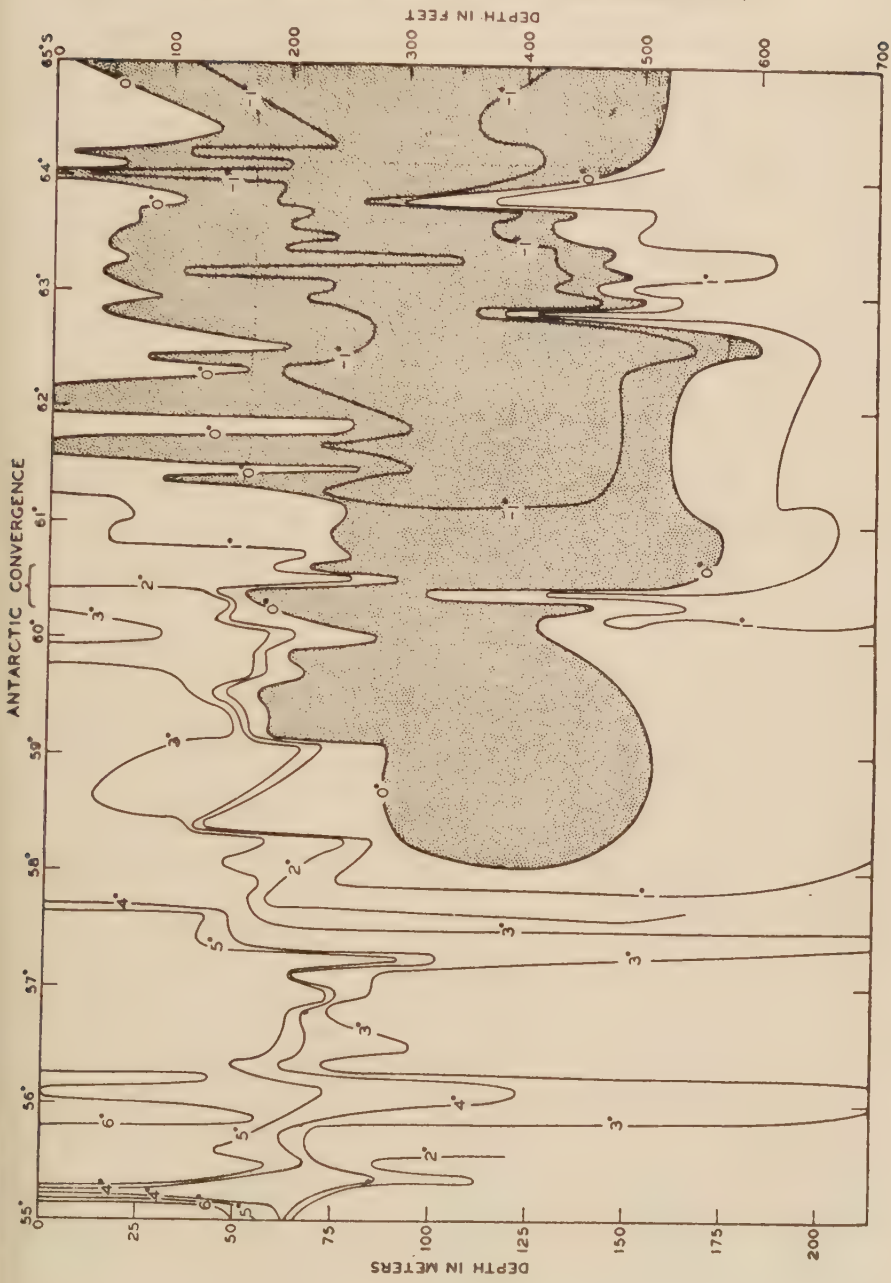


Figure 3. Vertical temperature sections across Antarctic convergence.

light and hence there is usually a subsurface diatom maximum. Schimper (Karsten, 1905) found diatom maxima at 40–80 m. in the Antarctic. Sverdrup, Johnson and Fleming (1942: 781) consider that this can be attributed only to sinking, since photosynthesis cannot occur in these latitudes below 50 m. Although there is some slight indication of a subsurface diatom maximum in the above data, it is not conclusive. Indeed, it is doubtful whether sunlight is ever sufficiently intense at these latitudes to become lethal to diatoms or inhibitory to their growth even at the extreme surface. The only conclusions that can be drawn from the present data are (a) that the euphotic and disphotic zones at these stations are extremely shallow, and (b) that probably the lower limit of the disphotic zone is about 200 ft.

ACKNOWLEDGMENTS

I would like to thank Robert Dietz and H. Mann of the Navy Electronics Laboratory, San Diego, who collected the material for this investigation. I am also indebted to E. C. La Fond of N. E. L. for the use of Fig. 3, and for obtaining permission from the Navy to publish this material.

APPENDIX

Surface Samples

Station	*Latitude (S)*	*Longitude*	*Temp. (° C.)*	*Date*
2	62° 2′	162° 3′ E.	−0.8	12/28/46
4	62° 5′	162° 0′ E.	1.0	12/29/46
6	62° 2′	159° 2′ E.	0.7	12/30/46
8	61° 8′	158° 2′ E.	1.8	12/30/46
9	61° 0′	156° 2′ E.	2.0	12/30/46
10	59° 3′	152° 0′ E.	1.9	12/31/46
12	59° 2′	150° 4′ E.	1.5	1/ 1/47
13	59° 5′	148° 8′ E.	1.0	1/ 2/47
14	60° 0′	150° 6′ E.	1.6	1/ 3/47
18	59° 9′	148° 8′ E.	1.3	1/ 5/47
24	61° 0′	140° 0′ E.	2.4	1/18/47
26	61° 0′	137° 3′ E.	1.9	1/20/47
28	65° 7′	141° 6′ E.	−0.4	1/22/47
30	64° 5′	156° 0′ E.	0.8	1/23/47
32	65° 5′	176° 1′ E.	2.1	1/25/47
34	66° 9′	173° 8′ W.	1.6	1/27/47
36	68° 1′	174° 7′ W.	−0.2	1/28/47
38	63° 5′	121° 8′ E.	1.0	2/ 7/47
40	60° 7′	29° 7′ E.	3.0	2/21/47
42	63° 9′	82° 3′ E.	−1.4	3/ 2/47
44	56° 6′	115° 7′ E.	4.6	3/ 6/47
46	55° 9′	117° 6′ E.	1.6	3/ 6/47
48	53° 4′	124° 7′ E.	5.7	3/ 7/47
49	47° 3′	135° 6′ E.	9.0	3/ 8/47
51	46° 1′	136° 5′ E.	10.9	3/ 9/47
53	40° 2′	143° 1′ E.	17.0	3/11/47
55	39° 5′	144° 2′ E.	18.1	3/11/47
59	32° 1′	165° 0′ E.	21.7	3/22/47

APPENDIX

Surface Samples

Station	*Latitude (S)*	*Longitude*	*Temp. (° C.)*	*Date*
61	29° 9′	170° 0′ E.	24.0	3/23/47
63	26° 3′	175° 6′ W.	24.3	3/24/47
65	22° 6′	179° 7′ W.	27.4	3/24/47
67	18° 4′	174° 9′ W.	29.0	3/25/47
70	14° 2′	170° 3′ W.	30.7	3/26/47
72	09° 9′	165° 9′ W.	30.0	3/27/47
74	03° 5′	159° 5′ W.	27.6	3/29/47
76	01° 6′ N.	154° 9′ W.	27.6	3/30/47

Hydrographic Stations

C1:	68° 43′ S.	174° 55′ W.	−0.5	1/30/47
C2:	59° 55′ S.	96° 45′ E.	2.8	2/11/47
C3:	60° 55′ S.	88° 55′ E.	2.6	2/13/47
C4:	59° 57′ S.	40° 30′ E.	2.5	2/19/47

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THE CONCEPTION OF ALKALINITY OR EXCESS BASE OF SEA WATER[1]

By

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There is full agreement on these facts: Sea water is slightly alkaline in its reaction towards suitable indicators, and the quantitative measure of this alkalinity may be expressed in terms of the amount of strong acid necessary to bring its reaction to some standard specified "endpoint." We call this property "alkalinity" if we describe the experimental phenomenon, or call it "excess base" if we try to interpret the observed facts and ascribe a cause. The term "buffer capacity" is unfortunate and should be dropped entirely.

It is proper to seek the cause of this property in what may be called the acid-base balance of the water, but there is a common misapprehension as to what we are talking about, because in chemical oceanography we are still clinging to conceptions which have been abandoned and replaced in the field of general chemistry. To be sure, the same misapprehension persists elsewhere, in some of the other applied fields of chemistry.

To illustrate the nature of the difficulty, let us examine some of the statements which appear in the literature.

Harvey, in his *Biological Chemistry and Physics of Sea Water*, says:

> The bases in sea water are slightly greater than the equivalent of stable acid radicals; there is a portion of *excess base or "alkali reserve"* which is in combination with carbonic acid. (Harvey, 1928: 64).

Later, in his *Recent Advances in the Chemistry & Biology of Sea Water* the same author states:

> The water contains basic radicles in excess of the equivalent of strong acid radicles. This excess base is itself equivalent to the bicarbonate, carbonate and borate ions in the water (Harvey, 1945: 52).
>
> Furthermore, some of the excess base becomes "bound" to borate ions which are set free from undissociated boric acid (Harvey, 1945: 54).
>
> The term 'Carbonate alkalinity' is used for that part of the excess base which is equivalent to the bicarbonate and carbonate ions (Harvey, 1945: 61).

[1] Contributions from the Scripps Institution of Oceanography, New Series, No. 418.

In the recent comprehensive textbook, *The Oceans*, we find:

> For a given sample of sea water the amount of a strong acid (usually HCl about 0.01 normal) necessary to reduce the pH to about 4.5 is independent of the total CO_2. This amount of acid is required to set free the weak acids whose anions have been bound against basic cations. It is therefore not only a measure of the quantity of anions of weak acids in the sample, but also of the cations balanced against them (Sverdrup, Johnson and Fleming, 1942: 195).

From Kalle's *Der Stoffhaushalt des Meeres:*

> Von einer gewöhnlichen Salzlösung, beispielsweise einer Kochsalzlösung, unterscheidet sich das Meerwasser in einem wesentlichen Punkt. Während in einer gewöhnlichen Salzlösung im allgemeinen die Menge der Kationen derjenigen der Anionen äquivalent ist, ist im Meerwasser diese Beziehung, soweit wir uns auf die Betrachtung der Ionen starker Basen und Säuren beschränken, nicht erfüllt. Wie Tabelle 7 (S. 38) zeigt, haben wir einen Überschuss von 2.38 Milliäquivalenten an Kationen pro kg Meerwasser (Kalle, 1945: 158–159).

Wattenberg not only defines excess base but relates the calcium ion concentration ion closely to it:

> Die Summe der im Meerwasser vorhandenen Kationen übertrifft nämlich die Summe der Anionen starker Säuren—beide ausgedrückt in Äquivalenten—um einen gewissen Betrag. Dieser "Basenüberschuss" ist die an Kohlensäure (als Karbonat und Bikarbonat) gebundene Basenmenge. Wird nun dem Wasser $CaCO_3$ entzogen oder zugeführt, so wird dadurch eine äquivalente Verminderung bzw. Vermehrung des Basenüberschusses, der sog. Alkalinität verursacht. Dieser Kalkstoffwechsel ist nun praktisch die einzige Ursache für die Veränderungen in der Alkalinität des Meerwassers, und es ist daher umgekehrt möglich, aus der Alkalinität den zugehörigen $CaCO_3$-Gehalt des Wassers zu berechnen (Wattenberg, 1930: 278).

In their paper *The Buffer Mechanism of Sea Water*, Moberg, Greenberg, Revelle and Allen say:

> By titratable base we mean the base balanced against weak acid radicals in sea water, or, stated in another way, the quantity of base which can be titrated with a strong acid when the titration is carried to a pH value at which all the weak acid radicals have been replaced by the acid added (Moberg, et al., 1934: 231).

Elsewhere, they refer to

> . . . the portion of the titratable base balanced by carbonic acid . . . (Moberg, et al., 1934: 261).

Greenberg, Moberg and Allen express themselves similarly:

> . . . we are using the expression "titratable base" to designate the base combined with weak acid radicals . . . (Greenberg, et al., 1932: 311).

Although West and Robinson (1941) make use of conceptions substantially the same as those which will be explained presently, they do not point out the general implications of them.

The above statements seem to agree on the following points:

1. The cations are bases. [Wattenberg (1930) followed this to a conclusion.]

2. The anions are at least "acid ions," if not actually acids.

3. The anions of weak acids are in some way inactivated by being "bound against" cations. Strong acid "replaces" these ions during the titration.

The tables referred to by Kalle (1945) list the principal cations, Na^+, Mg^{++}, Ca^{++}, K^+, Sr^{++}, in terms of equivalents and compare them with the anions, similarly expressed. The total equivalents of cations exceed the equivalents of anions, *but only if certain anions* (HCO_3^-, $H_2BO_3^-$, $CO_3^=$) *are left out of the list.*

In any electrolyte solution, of course, total anions equal total cations. What justification is there for neglecting the anions of weak acids? Just what is meant by "balancing" or "binding against"? How is this different from "binding with"? In at least three of the sources quoted above it is explicitly stated that some of the cations are *combined with* anions. If this were the case, the inactivation of the weak acid ions should also inactivate an equivalent of cations, and there would be no excess of base. But the idea of undissociated salt molecules (such as $NaHCO_3$ or KH_2BO_3) went out of style in physical chemistry some years ago. The current picture of an electrolyte solution, such as sea water, is one in which ions retain their independence rather than pair off with each other, although there is a diffuse interionic attraction of all the positive ions for all the negative. And there is no reason why a cation should be bound "against," or "by," or "with," an anion like bicarbonate any more than one like chloride.

The difficulty arises from the inconvenience, or utter failure, of our old ideas about the relation of acid to base. The same difficulty led to confusion in a totally different field, that of the so-called "ion-exchange" substances.

Certain natural and synthetic substances—first zeolites, and more recently certain resins—when immersed in solutions have the property of yielding up certain ions which they contain in exchange for other ions in the solution. The first of these substances were originally known as "base exchangers," since they exchanged sodium or potassium ions for calcium or magnesium. Others, later discovered, were called "acid exchangers" since they could exchange anions (then called "acid ions").

But presently it developed that the "base exchangers" could exchange calcium ions not only for sodium *but even for hydrogen ions*, which, according to the classical definition, is the one and only *acid*. Further, the "acid exchangers" were found to exchange sulfate ions not only for chloride *but even for hydroxyl*, which has classicially been thought the one and only *base*. Surely, acid cannot be exchanged for base!

All this confusion can readily be cleared up by turning to a revision which has taken place in recent years in our fundamental conceptions of acids and bases. The modern definitions or theory of acid and bases, although more general than the classical, afford much simpler explanations. We shall use such portions of the modern theory as are useful for our present purpose.

The properties of acids are ascribed to the unique character of the proton, or simple hydrogen ion (H^+), which, because of its small size, differs from other cations, the metals in general. The proton forms stable, individual unions with cations; with chloride, for example, the product HCl is a gas with a real molecular weight. (Contrast this with solid sodium chloride, in which no sodium ion is united with any particular chloride ion.) The proton is not irrevocably bound in such unions, however, but can separate to attach itself to any other entity (ion or neutral molecule) with which it forms a firmer union. Acids are defined as "proton donors" from which protons (H^+) can separate in this way. Protons separate *easily* from strong acids (HCl), with difficulty from weak ones (H_2CO_3).

Bases, on the other hand, are defined as "proton acceptors," substances (ions or neutral molecules) which can combine with protons. Protons form strong unions with strong bases, weak ones with weak bases.

It is evident from this that all anions are bases and that an acid *consists of a proton united with a base.* In a strong acid, like HCl, the proton is united with a weak base (Cl^-); in a weak acid, like H_2CO_3, the proton is united with a strong base (HCO_3^-, or $CO_3^=$, since two protons are involved).

Water itself is a weak base, combining with the proton of a strong acid, like HCl, to form Cl^- and H_3O^+, the hydronium ion or the hydrated proton. Water is also a weak acid, able to yield protons to strong bases, like $S^=$, or $CO_3^=$, or NH_2^- (to form HS^-, HCO_3^-, NH_3). All these exchanges are reversible, of course, and protons will distribute themselves between any bases that are present, in proportion to their strengths. It will be useless to go further into the details of these conceptions, which can be found in many modern textbooks of chemistry.

It should be noted that metal ions in solution (and doubtless all ions) are hydrated. For example, the cupric ion has the composition $Cu(H_2O)_4^{++}$, and the ferric $Fe(H_2O)_6^{+++}$, although there is some uncertainty about the number of water molecules coordinated in some cases. In a real sense, $Cu(H_2O)_4^{++}$ is a hydrogen compound containing protons, and elementary considerations of atomic structure would indicate that protons should be more easily separated from it than from the H_2O molecule. One must think of the water molecule as two protons, each of which is attached to an oxygen atom by sharing a pair of electrons. The oxygen atom has two more pairs of electrons, by which it can be "coordinated" to other atoms, molecules, or ions. When metal ions coordinate with water molecules in this way, the sharing of these electrons with the oxygen atom tends to draw in slightly the electrons which hold the protons to the oxygen. This loosens the H : O bond slightly and enables a proton to separate from the oxygen more easily than it will from an oxygen atom in an independent water molecule. Consequently, the "hydrated" metal ions have the properties of acids. Small ions, like iron and copper, coordinate the water molecules strongly and are therefore relatively strong acids; sodium or potassium, and other large ions, scarcely "polarize" the water molecules at all and are hardly any more effective as proton donors than water itself.

In place of the old classification, according to which cations and anions are considered "base ions" and "acid ions" respectively, the true situation is actually reversed: cations are in general *acids*, and anions in general *bases*.

Now it can be readily understood that in a water solution containing $Cu(H_2O)_4^{++}$ and Cl^- ions there is a predominance of acid over base. Although their equivalent concentrations will be the same, the copper ion is more effective as an acid than is the chloride as a base. It can yield a proton to an added indicator more readily than the chloride will take one from the indicator, and the well known color change takes place. The solution contains "excess acid."

In a solution containing $Na(H_2O)_x^+$ and HCO_3^- ions, the bicarbonate is more effective as a base than the sodium (in equivalent concentration) as an acid, the solution has an alkaline reaction, and we have all the evidences of *excess base*.

In a neutral solution of sodium chloride we have not only equivalent concentrations of anion and cation but also equal acid and base effectiveness. (The term "activity" must be avoided, since it has another technical significance.)

"Excess base," therefore, refers more particularly to relative acid

and base strength than to relative concentration. We can now deal with the actual situation in sea water.

The cations (acids) present are: $Na(H_2O)_x^+$, $Mg(H_2O)_x^{++}$, $Ca(H_2O)_x^{++}$, $K(H_2O)_x^+$, $Sr(H_2O)_x^{++}$. (The water of hydration is usually omitted when writing the formulas.) Of these only the magnesium ion has any appreciable power as an acid, and even this is too small to be significant. Cations which might be effective acids, $Fe(H_2O)_6^{+++}$ or $Cu(H_2O)_4^{++}$, and of course H^+ (or H_3O^+), are in too low concentration to be important. The anions (bases) present are: Cl^-, $SO_4^=$, Br^-, HCO_3^-, $H_2BO_3^-$, $CO_3^=$. The first three are too weak as bases to be significant; it is to the last three that the alkalinity of the water is due. Phosphate and silicate ions, moderately strong bases, are in insignificant concentration.

The "alkalinity" of the water is the result of the predominance of base effectiveness over acid effectiveness. When we titrate by adding HCl we choose an endpoint at which the HCO_3^-, $H_2BO_3^-$ and $CO_3^=$ are completely combined with protons to form H_2CO_3 and H_3BO_3. Only the relatively strong acids and bases are involved, so that chloride, bromide, sulfate, and the principal metal cations are unimportant. Hydrogen and hydroxyl ions, although respectively strong acid and base, are too dilute. So that, finally, our definition of excess base, in terms of equivalents of acid added,

$$A = [HCO_3^-] + 2\,[CO_3^=] + [H_2BO_3^-]\,,$$

is an exact definition of what we *mean* by excess base, not something which is merely *equivalent* to it.

This is entirely incompatible with Gripenberg's (1936) statement that while the quantities on the right of the above equation vary with the hydrogen ion concentration the excess base is independent of it. Her statement is the result of assuming that excess base is a *cation concentration* and it is hard to see how it can be true even according to the older view. Our criterion of the presence of excess base is the fact that acid must be added to the water to bring the pH to an endpoint of, say, 5. Obviously, if the original pH of the water were 5, by definition there would be no excess base in it.

Finally, the effect of calcium carbonate precipitation upon the alkalinity is the result of the removal not of calcium ions but of carbonate, which of course is chemically equivalent.

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A CAMERA FOR PRODUCING ONE-DIMENSIONAL REDUCTION IN NARROW RECORDS[1]

By

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Many instruments yield long, narrow records which are of an awkward shape for reproduction. In the course of work under Navy contract NObs-2083, numerous fathograms were obtained which showed the diurnal movements of the "deep scattering layer." This layer is believed to be of planktonic origin (J. B. Hersey and H. B. Moore, 1948).[2] The part of the fathogram which includes the scattering layer is about two inches deep, while a day's record is three feet long. The instrument described here combines photographic reproduction, which is preferable in this case, with the desired change in the ratios of the vertical and horizontal scales. Similar records appear likely to be of use to geologists in studying long stretches of the ocean bottom.

The paper record is wound by a toothed drum under a lucite sheet which fills the field of a 5 x 4-inch film in a camera (Fig. 1). There is a light-tight case from the camera lens to the lucite sheet, the part of this next to the lens being fixed, the rest being mounted on a vertically-sliding carriage. Close to the lucite, the case narrows to an adjustable horizontal slit one millimeter in diameter. Two 100-watt lamps are mounted on the carriage in housings which concentrate the light on the part of the fathogram opposite the slit. The carriage slides on vertical guides, and is slowly lowered by a suspending string. This string is unwound from a smaller drum fixed on the same axle on which the record-driving drum rotates. The ratios of the diameters of these drums is so chosen that, as the slit descends and scans the length of the lucite sheet, a little over three feet of fathogram is drawn past it.

Fig. 2A shows a normal photograph of a day's fathogram, reduced to reproducible size. Fig. 2B shows the same length of this record as reproduced by the slit camera, but with only the upper part containing the scattering layer included. Not only are the details of the diurnal migration of the layer much clearer in the latter, but also the distortion produced by the slope and curvature of the vertical coordinates is much reduced. Details of lettering on the original are,

[1] Contribution No. 448 from Woods Hole Oceanographic Institution.

[2] Progress report on scattering layer observations in the Atlantic Ocean, Trans. Amer. geophys. Un., *29* (3): 341–354, 1948.

of course, lost in the contraction, but a label fixed to the lucite sheet may be included in the negative if desired.

While no new principle is involved in the apparatus, it is proving so useful that a description appears justified. It could readily be modified to take other types of records, or to produce any desired degree of contraction.

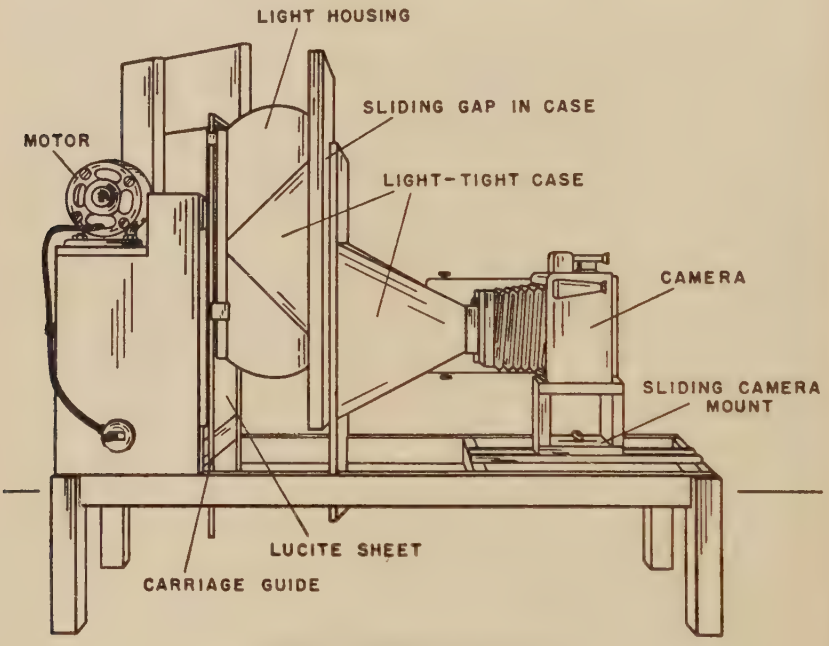

Figure 1. Elevation of camera.

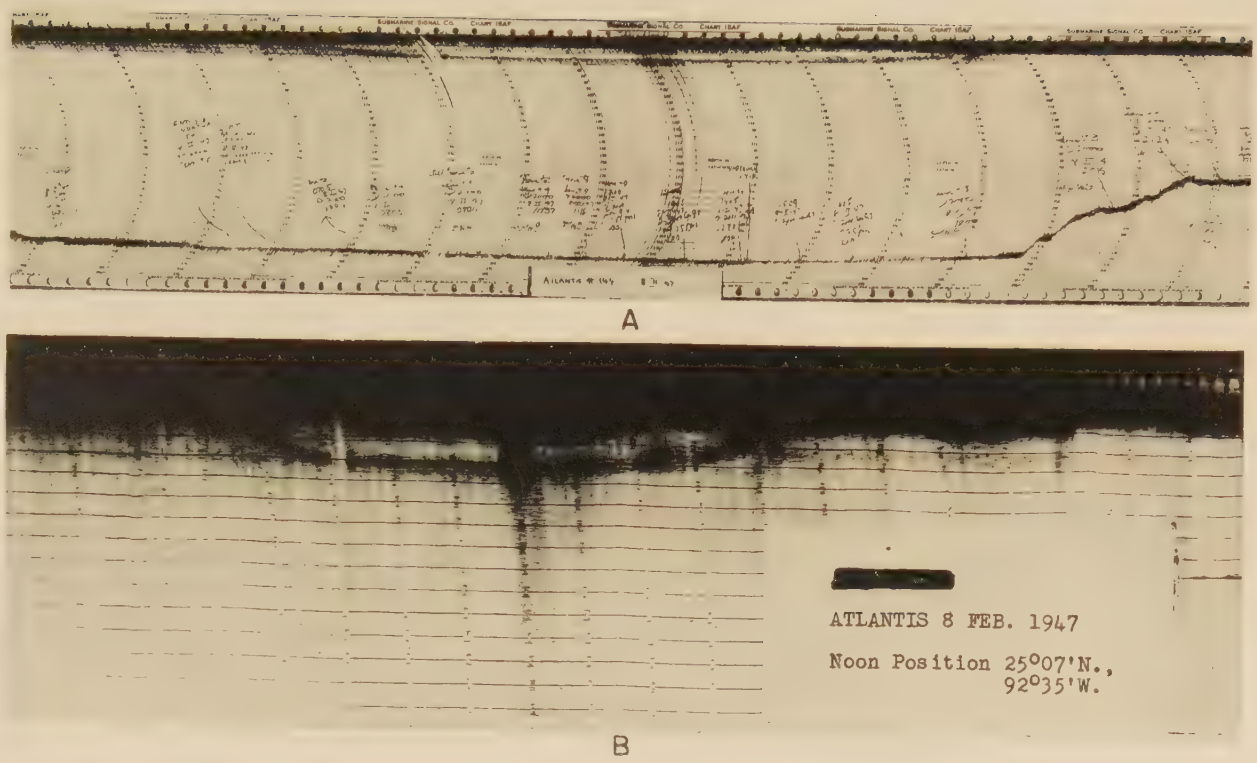

Figure 2A. Fathometer trace with normal dimensions, X 1/5. 2B. Upper part of above fathometer trace reproduced with slit camera.

TRAJECTORIES OF SMALL BODIES SINKING SLOWLY THROUGH CONVECTION CELLS[1]

By

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INTRODUCTION

Mr. J. C. Neess of the University of Wisconsin has indicated to the writer in a personal communication that he has often observed a greater variability in plankton tows taken up or down wind in a lake than when made across wind. He suggested that this might be due to convective or wind-induced cellular motion in the water, which in some manner should act to concentrate plankton in linear arrays in the direction of the wind, thus leaving relatively clear lanes between. This fact suggested that it might be of interest to set up a simple cell analytically and to see what kinds of paths or trajectories the particles of various settling velocities would describe.

The existence of long strip wind-induced cellular motion in lakes and oceans has been demonstrated (Langmuir, 1938; Woodcock, 1941). The nature of the trajectories should not depend necessarily on the nature of the forces producing the cellular motion, so that the results should apply equally well to thermally-induced cellular motion. The layer of wind-induced or thermally-induced strip cells may be thought of in the following way. The layer is divided into a number of strips (or cells) lying side by side with their lengths parallel to the wind. The water in each cell is rotating around the central axis of each cell, the sense of rotation in any given cell being opposite to that of its immediate neighbors, much like the rotation of a long train of gears. The boundaries of these cells are regions of sinking and rising water alternately. In addition to the rotating movement there is a movement in the direction of the wind so that a given particle of water describes a helix with axis horizontal and in the direction of the wind.

Fig. 1 shows a cross section view of two neighboring cells. The arrows indicate the direction of water movement in the plane perpendicular to the wind direction; the curved lines are streamlines. The motion of the water in the direction of the wind clearly has no effect

[1] Contribution No. 469 from the Woods Hole Oceanographic Institution.

[2] The writer wishes to thank Dr. C.-G. Rossby for reading this paper and suggesting several important improvements.

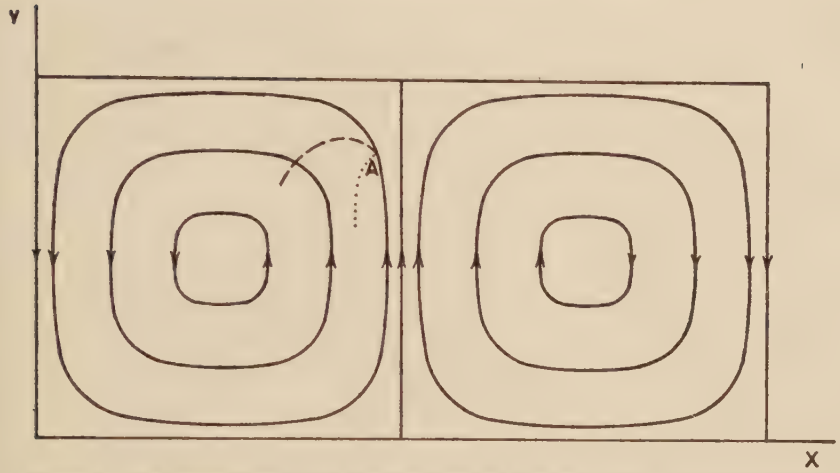

Figure 1. The streamlines of an idealized vertical section across a pair of convection cells. The arrows show the direction of the water flow.

upon the trajectory of a particle immersed in the cell except to move it uniformly in the direction of the wind. We may consider the problem as essentially two dimensional.

A small body whose density is the same as that of the water will have no tendency to settle. Therefore its trajectory will lie along the streamlines of Fig. 1—in other words it will simply move along with the water. Particles whose densities are greater than that of the water will tend to sink with a constant settling velocity, and if placed in still water they will tend to settle vertically downward in straight line trajectories. In case of convective motion, as shown in Fig. 1, such a heavy particle introduced at point A cannot rise along the streamline as would a particle with zero settling velocity; rather, it will start to fall immediately (for example, along the dotted line), and, if heavy enough, will fall through the bottom of the convective layer. A particle with a smaller settling velocity, if placed initially at point A, will begin to rise at first because the rising current is strong there, but eventually it will be swept horizontally to a region where the upward velocity is less and hence it will fall away (for example, along the dashed line).

One naturally wonders if this particle will be caught up again into the ascending current and so execute an endless number of circuits, or whether it is bound eventually to fall out of the layer. As a matter of fact, one begins to wonder whether all particles with a settling velocity—no matter how small—will eventuallly fall out of the con-

vective layer. This is not the case, however, as will be shown in the following section.

THEORETICAL TREATMENT

A system of axes is fixed to the layer as shown in Fig. 1. The coordinates of a particle are (x, y), both of which are functions of the time t; $x(t)$, $y(t)$.

The horizontal velocity of the particle is dx/dt, the vertical velocity dy/dt. The fluid motion may be specified by a stream function ψ, which, in general, is quite arbitrary. The horizontal and vertical velocities of the water are $\partial\psi/\partial y$ and $-\partial\psi/\partial x$ respectively.

If the settling velocity is denoted by V, we know that

$$\frac{dx}{dt} = \frac{\partial\psi}{\partial y}; \frac{\partial y}{\partial t} = -\frac{\partial\psi}{\partial x} - V.$$

The trajectories may be specified by a function ψ_1 where

$$\frac{dx}{dt} = \frac{\partial\psi_1}{\partial y}; \frac{dy}{dt} = -\frac{\partial\psi_1}{\partial x}.$$

The function ψ_1 is therefore given by the following expression

$$\psi_1 = \psi + Vx.$$

The trajectory of a particle is a curve along which ψ_1 is constant. The result is quite general. In the case of convection cells the simplest stream function to consider is

$$\psi = \psi_0 \sin x \sin y.$$

The streamlines of Fig. 1 were constructed from this function.

In this case the trajectories are given by

$$\frac{\psi_1}{\psi_0} = \sin x \sin y + Rx,$$

where the quantity R is defined by

$$R = V/\psi_0.$$

The trajectories shown in Figs. 2, 3, and 4 were constructed from this function.

DISCUSSION OF RESULTS

It is convenient to discuss the trajectories for different settling velocities in terms of the quantity R: the ratio of the settling velocity to the maximum upward water velocity.

The case where $R \geqslant 1$. If R is quite large the trajectories are essentially straight vertical lines. As R approaches unity the trajectories become curved. Fig. 2 is drawn for the limiting case $R = 1$. The particles all settle out, but as they approach the region of maximum upward motion they diverge and fall more slowly, as if to avoid that region.

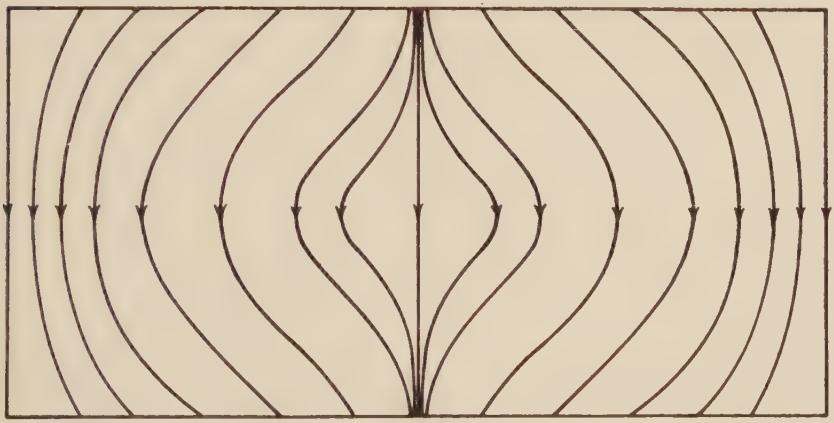

Figure 2. The trajectories of small bodies whose sinking velocity is just sufficient to insure that they all settle out.

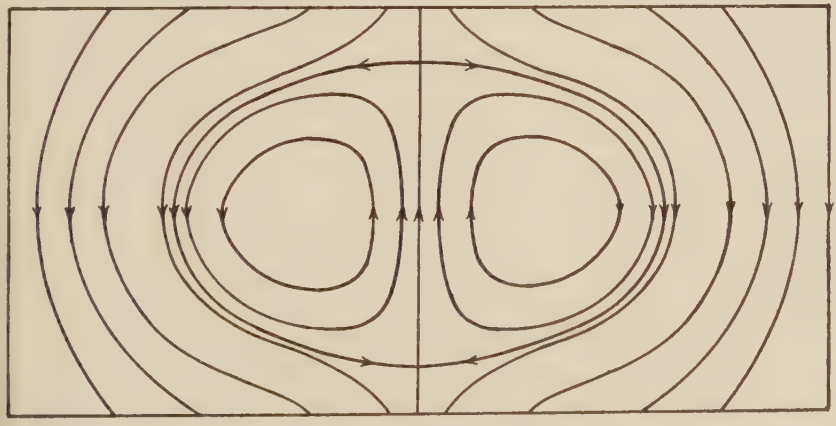

Figure 3. The trajectories of small bodies whose sinking velocity is just one-half of those in Fig. 2. The closed trajectories lie within a region conveniently called the region of retention.

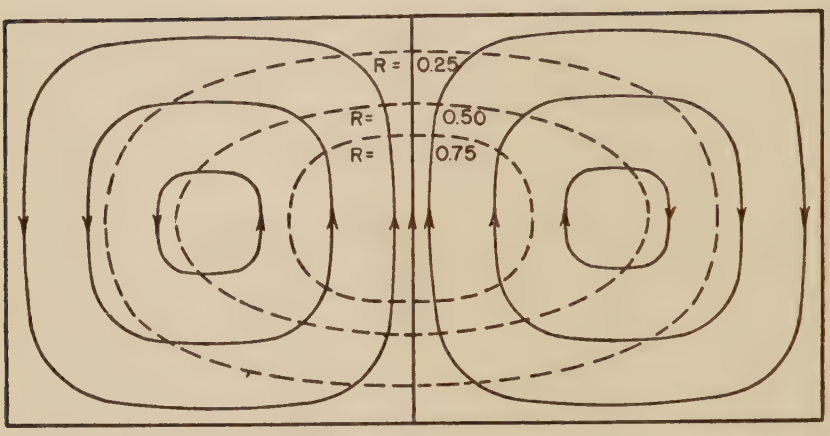

Figure 4. Solid lines are streamlines of the convective motion as shown in Fig. 1. Dashed lines are the boundaries of the regions of retention for various values of the number R.

The case where $1 > R > 0$: There are regions of the fluid motion where the particles, though constantly falling relative to the water, are moved upward through the convective layer. Fig. 3 is drawn for the case $R = 0.5$. The interesting feature of this figure is that there are closed trajectories in the upward current. A particle placed on one of these trajectories makes an endless number of circuits and does not fall out of the convective layer despite the fact that it is always falling relative to the fluid. The trajectories more remote from the region of maximum upward velocity are not closed. Particles placed on one of these trajectories fall out of the convective layer.

If particles are strewn at random into the cell, shown in Fig. 4, some will fall out while others are retained in closed circuits. After awhile two distinctly different regions in the fluid will be clearly visible: (i) a region which has lost all of its particles and (ii) a region of closed trajectories which has retained its particles in closed trajectories. The latter region may be spoken of as the "region of retention."

The region of retention becomes larger as R approaches zero. The boundaries of the regions of retention for values of R, equal to 0.25, 0.50, and 0.75, are shown in Fig. 4.

If particles of different settling velocities are introduced simultaneously, a sorting process ensues, in which heavier ones are concentrated near to the upward water currents and lighter ones extend to greater distances from the upward currents.

The population density of particles of a given R will be zero outside the region of retention, but it will not be uniform within that region.

Near the upward currents the space velocity of the particles is smaller than in other portions of the retention region, and therefore, from the principle of continuity, the density of population will be greater in the center of the regions of retention.

In actual convection cells there is always some degree of turbulence present, so that there will always be some turbulent exchange across trajectories of particles. In such a case a region of retention must gradually lose its particles by turbulent exchange with the outside region, the rate of loss depending upon the degree of turbulence.

If a sharp density increase occurs directly beneath the convective layer, particles that have a settling velocity in the convective layer will not necessarily sink through the underlying water. In nonturbulent cellular convection this would mean that there was an accumulation along the x-axis (Fig. 1) of those particles which were not in the region of retention, the accumulation being particularly dense on the x-axis directly under the regions of retention. In the presence of turbulence there will be a slight turbulent exchange between this accumulation of particles on the bottom of the convective layer and those in the region of retention. On the whole, an equilibrium would be established with a certain fraction of the population in the region of retention, most of the remainder on the x-axis directly under the region of retention, and a very small fraction moving en route between these two centers of population through the "clear" region.

Particles less dense than water have an upward velocity relative to the water (e. g., pelagic sargassum, providing settling is independent of depth). They cannot escape through the free surface. It would be evident that the preceding discussion may be applied to this case by simply inverting the picture.

There is a possibility that the method here advanced might be applicable to problems in convective clouds.

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A PRECISE DETERMINATION OF CHLORINITY OF SEA WATER USING THE Ag-AgCl INDICATOR ELECTRODE

By

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A knowledge of the relative currents of the oceans depends to a large extent upon a knowledge of the distribution of mass. Measurements of temperature and chlorinity[3] are made to furnish the necessary data for the computations of the density. The thermometers used are accurate to ±0.02° C. For an equal degree of accuracy, the chlorinity measurements should be made to ±0.001 °/₀₀ Cl. For routine work the Mohr titration with an accuracy of ±0.01 °/₀₀ Cl is used. This limit of accuracy is not important except for measurements where small chlorinity differences are significant (e. g., in the deep sea). A method suitable for the latter work, to replace the Volhard method used in the preparation of standard solutions, is desirable. Potentiometric titrations of halide are known to be highly precise (4). West and Robinson (7) applied such a method to the determination of chlorinity and reported a precision of better than ±0.01%. These authors used bimetallic electrodes for their end-point indicators. While engaged in preparing secondary standard chloride solutions, we had occasion to use certain bimetallic electrode couples but were unable to obtain satisfactory results. As a consequence, further investigation of the method was undertaken and satisfactory results were obtained in using silver-silver chloride electrode in combination with an enclosed reference electrode. The data are presented herewith.

Reagents

Silver Nitrate: Two solutions of approximately 0.22N silver nitrate were stored in dark brown bottles. A weighed portion of each of these was diluted ten-fold in calibrated volumetric glassware.

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[3] Chlorinity (°/₀₀ Cl) is defined as the weight in grams (*in vacuo*) of the halides contained in one kilogram of sea water (*in vacuo*) when all the bromides and iodides have been replaced by chlorides.

Copenhagen Standard Sea Water: Samples of the water bottled by the Hydrographic Laboratories of Copenhagen in 1937, and labeled with the chlorinity 19.393 °/₀₀, were used as one set of standards. This water had been originally standardized against silver nitrate, prepared from atomic weight silver by the Volhard procedure (3), with a reported accuracy of ±0.0005%.

Sodium Chloride: Merck blue label salt was recrystallized once from its saturated solution with HCl gas and once from a saturated solution with alcohol. The alcohol was purified by redistillation from alkaline silver nitrate. The salt was dried from four to eight hours in an electric furnace at the crackling temperature (500–600° C.) to remove the last traces of water.

Potassium Chromate Indicator: A saturated solution of K_2CrO_4 was prepared chloride free.

Water: Distilled water was redistilled from alkaline permanganate solution.

Apparatus

The measuring component of the end-point indicator system was the direct reading vacuum-tube voltmeter develcped by Anderson and Hindman (1).

Various combinations of the following metallic electrodes were investigated. Tungsten, chromium and gold electrodes were prepared by electrolysis of solutions of their salts using platinum foil anodes and cathodes. For the silver electrodes silver wires were employed. A graphite rod was used as the carbon electrode.

Silver-silver chloride electrodes were prepared from silver wire by electrolysis in 0.1 molar sodium chloride solution at a current density of 0.001 amp. per electrode. Care was taken to keep the layer of silver chloride as thin as possible. As a reference half-cell to be used with this electrode, a wick type electrode similar to the calomel electrode of ZoBell and Rittenberg (8) was entirely satisfactory. In this type of electrode, contact with the external solution is made through a small asbestos fiber sealed into the outer glass envelope. A platinum wire immersed in saturated potassium nitrate solution was used, however, in place of the internal calomel cell of the above authors. The electrode has numerous advantages; it is easily constructed, rugged and has had no perceptible contamination or solution leakage in several months of usage.

Procedure

The titration procedure was essentially the same as that used by West and Robinson (7). For standardizations using the Copenhagen

water, a 15 ml sample was delivered from a pipette into a 100 ml beaker and weighed. A quantity of concentrated silver nitrate solution approximately 0.25 ‰ Cl (1.2%) less than equivalent to this amount of chloride was added rapidly from a burette and the beaker was again weighed. The solution was covered with a watch glass during the weighing to minimize evaporation. The beaker was then transferred to the titration assembly and mechanically agitated for several minutes, after which time the titration was completed by addition of the dilute silver nitrate from a microburette. The precision of the end-point was ±0.01 ml, corresponding to a maximum error of approximately ±0.0005%.

For the check standardizations, dry sodium chloride was weighed out, dissolved in about 25 ml of water, the silver nitrate added, and the titrations completed as described above. All weights were corrected to vacuo.

RESULTS

It was found, in general, that none of the bimetallic couples tested gave satisfactory results. While a break could be observed at first at the end-point of the titration, after a few minutes the electrodes tended to become passive. In every case it was noted that the electrode surfaces were discolored, probably from a coat of silver chloride. A similar explanation has been offered by Van Name and Fenwick (6) for the behavior of ignited platinum electrodes in titrations of silver nitrate with sodium chloride. The bimetallic electrodes used by us also suffered from another disadvantage, namely, that their potential changes were never as large as those observed when reversible electrodes were used. The actual potential changes were approximately one-tenth as large when the bimetallic electrodes were employed as when a silver-silver chloride indicator electrode was used. Since the silver-silver chloride and reference electrodes are easy to prepare, there is no advantage in using irreversible systems. The silver-silver chloride electrodes do become sluggish after considerable use. This is due to a gradual thickening of the layer of the salt on the surface of the electrode. If the surfaces are wiped with a clean cloth before putting the electrodes away after work, they may be preserved more or less indefinitely. Silver electrodes are also satisfactory but slightly more erratic in behavior than those of silver-silver chloride.

The results of the potentiometric standardizations of the silver nitrate solutions with the Copenhagen water and sodium chloride are shown in Table I. In computing the chloride equivalence of Copenhagen water it is necessary to correct for the difference in atomic weights between the present values and those of the original (1902)

TABLE I.—Standardization of Silver Nitrate

Copenhagen Water	*Sodium Chloride*	*Copenhagen Water*	*Sodium Chloride*
Silver Nitrate No. 1		*Silver Nitrate No. 2*	
mgm. Cl *per gm.*	$AgNO_3$ *solution*	*mgm.* Cl *per gm.*	$AgNO_3$ *solution*
7.4712	7.4710	7.4658	7.4665
7.4701	7.4724	7.4658	7.4653
7.4721	7.4705	7.4655	7.4652
7.4712		7.4652	
7.4710			
Average 7.4711	7.4713	7.4656	7.4657
Av. deviation ±.0005	±.0007	±.0002	±.0006

potassium chloride standard which furnishes the unvarying reference value for chlorinity determination. The chloride equivalent is 1.00045‰ Cl (3). The maximum average deviation from the mean of the checks is ±0.009%. The best results, using the potentiometric method, reported in the literature are those of Lange and Schwartz (4) who were able to obtain a precision of about ±0.003%. The agreement between the Copenhagen water and sodium chloride standardizations was excellent, confirming the findings of Thompson (5) that secondary standard waters may be prepared using sodium chloride as primary standard.

Table II indicates comparative data on the modified potentiometric and Mohr methods. In this case weight procedures as outlined above were used for both indicators. The results show that the precision of the two methods is about the same. It is probable that the difference in chlorinity found by the two methods can be ascribed to an absolute error in determining the true end-point by the Mohr procedure.

Investigations were also made of the degree of precision obtainable when the potentiometric method was used in routine chlorinity determination. Table III shows the results of a series of determinations made in quadruplicate. The potentiometric results were obtained by us. The comparison results were obtained by trained technicians following the routine procedure used in this laboratory. This procedure differs from that described by Helland-Hansen (2) in that mechanical stirring is employed. The precision is greatly improved by this departure. The potentiometric procedure was identical with the exception of the end-point indicator. The results show that the deviations in check runs are smaller by the potentiometric method. However, other sources of error, such as temperature changes, burette

and pipette drainage effects, are sufficient to make the accuracy of the determinations about the same for both methods. Where high accuracy is desired, and where precautions are taken to minimize these sources of error, the potentiometric end-point indicator is found to give considerably more reliable results.

TABLE II.—Precise Chlorinity Determinations by the Mohr and Potentiometric Methods

Sea Water	‰ Cl *potentiometric*	*Average deviation from mean*	‰ Cl *Mohr*	*Average deviation from mean*
No. 3	18.426		18.422	
	18.429		18.418	
	18.426		18.420	
	Av. 18.427	±0.0013	18.420	±0.0013
No. 27	19.016		19.010	
	19.015		19.012	
	Av. 19.015	±0.0005	19.011	±0.001

TABLE III.—Routine Volumetric Determination of Chlorinity

Depth	*Mohr Chlorinities*			*Potentiometric Chlorinities*		
(*m*)	*1st*	*2nd*	*Av.*	*1st*	*2nd*	*Av.*
0	18.475	18.470	18.473	18.486	18.486	18.486
10	18.470	18.475	18.473	18.497	18.495	18.496
20	18.405	18.400	18.403	18.400	18.402	18.401
30	18.360	18.360	18.360	18.366	18.365	18.366
40	18.310	18.320	18.315	18.317	18.317	18.317
50	18.310	18.320	18.315	18.317	18.314	18.316
75	18.465	18.475	18.470	18.472	18.475	18.474
100	18.555	18.550	18.553	18.549	18.550	18.550
150	18.745	18.730	18.738	18.751	18.753	18.752
200	18.850	18.840	18.845	18.854	18.853	18.854
250	18.880	18.880	18.880	18.895	18.895	18.895
300	18.945	18.935	18.940	18.954	18.954	18.954
400	18.960	18.960	18.960	18.978	18.975	18.977
500	18.980	18.975	18.978	18.999	19.001	19.000
600	19.005	18.995	19.000	19.022	19.022	19.022
Average diff. between duplicates			0.007			0.0015

SUMMARY AND CONCLUSIONS

A potentiometric method for precise chlorinity determinations is described. Standardization of two silver nitrate solutions, using Copenhagen water as a secondary standard as well as pure sodium chloride as a primary standard, gave results agreeing to ±.002% with a probable error of ±.007%. The suitability of sodium chloride as a primary standard in the preparation of secondary standard sea waters is thus confirmed.

When the method was used to determine the chlorinity of sea water, a probable error of ±.005% is obtained. Used in the routine titration of sea water, a probable error of ±.008% is obtained as compared to ±.040% for the standard Mohr titration procedure.

Certain bimetallic electrodes were found to be inferior in performance and reliability to the reversible silver-silver chloride electrode.

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EXPERIMENTS IN THE FERTILIZATION OF A SALT WATER POND[1]

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It has long been recognized that the biological productivity of the sea depends primarily upon the nutrition of the phytoplankton. The aim of these experiments was to study this basic process in the cycle of production by the artificial increase of those plant nutrients most likely to become limiting. For our purpose a body of water was required which was large enough to be representative without excessive water exchange due to tidal action, yet small enough to permit an adequately conclusive study. Having selected a salt pond which met these requirements, the specific objectives were 1) to determine whether it is feasible to raise and maintain at high levels the concentrations of phosphate and nitrate by the addition of commercial fertilizers, and 2) to observe the effects of such increases upon the standing crop of phytoplankton.

A considerable body of evidence from laboratory culture work (e. g., Riley, 1943) and from fresh-water fish-pond management (e. g., Swingle and Smith, 1938) indicates that the concentrations of several nutrient salts may limit phytoplankton production simultaneously. For this reason frequently the maximal growth cannot be produced by supplying only one or two of the deficient elements. However, since our primary concern was to study the effects of different nutrients rather than to increase plankton production, we have confined our experiments to two substances, namely phosphate and nitrate, whose concentrations in the sea are limiting.

Compared with the work in fresh waters, fertilization of salt water areas has been rarely attempted. Evermann (1904), Gaarder (1932), Gaarder and Spärck (1932), and Gaarder and Alvsaker (1941) have fertilized partially enclosed bodies of salt water to increase the production of oysters. Frequent reference will be made to the work of Gross, *et al.*, who have improved the production of flatfishes in semi-enclosed sea lochs in Scotland (Gross, 1947; Orr, 1947; Marshall, 1947).

[1] Contribution No. 466 from the Woods Hole Oceanographic Institution.

Edmondson and Edmondson (1947) discuss salt water fertilization experiments conducted in concrete tanks and in a natural pond.

The work of the Edmondsons and the present study form parts of a general study of productivity in marine waters, under the direction of George L. Clarke. Most of the plankton counts were made by Miss Mary Goffin and Theodore R. Rice. I am also indebted to George A. Bartholomew and Thomas F. Dolan for assistance in various chemical determinations.

METHODS

The water samples for all determinations were generally collected between 9 a. m. and noon, from a depth of a few inches below the surface.

Salinity was calculated from density measured with a special hydrometer.

Hydrogen-ion concentration was determined with a Hellige comparator and corrected for salt error (Wattenberg, 1937).

Inorganic phosphate concentration, determined by the modified Deniges-Atkins method (Wattenberg, 1937), was measured in a Klett-Summerson photoelectric colorimeter. Factors were applied for correction of salt error as determined by calibration. Concentrations are expressed as microgram-atoms of phosphate phosphorus per liter (μg.-at. PO_4 P/l.).

"Nitrate" was measured by Zwicker and Robinson's (1944) method, which does not distinguish between nitrate and nitrite. The measurements were made with a Klett-Summerson photoelectric colorimeter, using either filter no. 42 or no. 54. Concentrations are expressed as microgram-atoms of nitrate nitrogen per liter (μg.-at. NO_3 N/l.). For lack of the necessary strychnidine reagent, nitrate was not measured until late June 1947.

Zwicker and Robinson warn that inorganic reducing agents or high concentrations of plankton or of dissolved organic matter may inhibit color development in this test. The observed or probable presence of all three of these factors in the pond may explain the consistently low readings of nitrate which were obtained except during fertilization experiments. Due to these possible sources of error and to the fact that high blanks frequently necessitated the application of large correction factors, no great reliance should be placed on the absolute values obtained.

Phytoplankton. For the quantitative analysis of the phytoplankton, two different procedures were employed. In 1946 water samples were preserved with 3% formalin, the plankton counted after settling and

centrifuging. From the numbers and mean dimensions of the cells of each species present, the total cell volume of the phytoplankton in each sample was computed.

However, this method proved so laborious that in April 1947 a different procedure was adopted. The phytoplankton was sampled by measuring the chlorophyll concentration, with qualitative microscopic examination to identify the organisms present and only occasional quantitative estimation of cell numbers and volumes. For the chlorophyll determination the plankton in a one or two liter sample was concentrated by either of two methods: 1) by filtering in a modified Seitz filter through Whatman No. 42 paper covered with a layer of barium sulfate (Redfield, Smith and Ketchum, 1937), or 2) by using a Foerst continuous centrifuge, bringing the catch to dryness by filtering through barium sulfate on Whatman no. 42. The second method resulted in chlorophyll readings that were only about 95% as great as those obtained by the first method, but it required far less time. The remaining procedure for the chlorophyll determination is the same as that followed by Edmondson and Edmondson (1947: 231), who give the transmission spectra of the Klett filters no. 66 and no. 69 and discuss their use in chlorophyll measurements. The Klett colorimeter and filter no. 66, with which chlorophyll concentrations in the present work were determined, were calibrated against the instrument and filter used by the Edmondsons. The amount of chlorophyll is expressed as milligrams of chlorophyll *a* per cubic meter.

The two methods of phytoplankton measurement are compared in Fig. 1, which shows the relation between chlorophyll concentration and calculated total cell volume in 43 pairs of duplicate samples which were analyzed by both procedures. The least squares line has been fitted to the data; the correlation coefficient is 0.908. This degree of agreement is surprising when one considers that the samples were taken during the months April–August from populations which varied in their species composition and physiological state. The sample showing an abnormally high chlorophyll/volume ratio (chlorophyll = 44.25 mg./m^3, volume = 4.136 ml./m^3) was collected on a day when unusually high wave action roiled the water. On the basis of unpublished work of Denis L. Fox (in litt.) it appears likely that phaeophytin and other chlorophyll derivatives, which are relatively stable and tend to accumulate in bottom muds and which absorb some light at 660μ, may have interfered with the chlorophyll determination in this sample.

Note that the agreement between the two methods is nearly as close at high values as at low. This is probably due to the fact that in all samples with a calculated total cell volume greater than 15 ml./m^3, by far the greatest fraction of the total volume was contributed by large

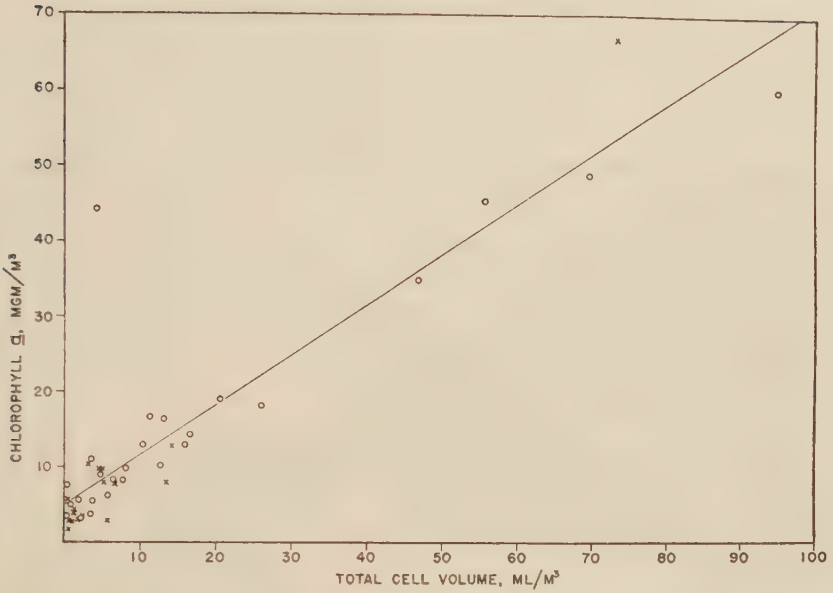

Figure 1. The relation between concentration of chlorophyll *a* and calculated total cell volume in 43 pairs of duplicate phytoplankton samples.

X's = samples preserved in 3% formalin before enumeration and measurement of cells. Circles = samples in which cells were counted and measured in the fresh state.

cells which probably belonged to the same species (genus *Peridinium*). The same predominance of apparently the same species of *Peridinium* in all other samples with a total cell volume greater than 15 ml./m³ makes it fairly safe to conclude that had these samples been tested for chlorophyll they would have shown approximately the same volume to chlorophyll relationship as is illustrated in Fig. 1. This relationship is chlorophyll *a* (mg./m³) = 5.035 + 0.6647 × volume (ml./m³). In view of the high correlation between the two methods of plankton measurement and the desirability of presenting all the data in common units for the sake of intercomparison, all volumetric measurements will be expressed in terms of their chlorophyll equivalents, as calculated by this equation. Due to the quantity 5.035 in the equation, such a transliteration produces an artificial absence of chlorophyll values less than that number. But this distortion is not considered serious, since it affects only the lower and consequently less interesting range of values where the percentage of error is probably highest.

HYDROGRAPHY AND PHYTOPLANKTON

Little Harbor, an arm of the sea situated in Cohasset, Massachusetts, is connected with the open ocean by a narrow neck at its eastern end, as shown in Fig. 2. The northwest portion of Little Harbor, enlarged in Fig. 3, is the pond with which the present study is concerned.

Figure 2. Little Harbor, Cohasset, Massachusetts (traced from aerial photograph).

The narrow southern extremity, which is the pond's only connection with the main body of Little Harbor, is closed by a dam. The dam is provided with a check gate about ten feet long and three feet deep, which is suspended from a hinge in such a way that it is pushed inward and raised by the rising tide, admitting the inflowing water rapidly. The ebbing tide holds the check gate closed while pouring

out over the top of it; this continues only as long as the water level of the pond is higher than the top of the dam. As a result, the tide flows in for only about two hours and out for about ten hours. The average difference between high and low tide levels in the pond is only 0.22 m., while in other parts of Little Harbor this difference is nearly 3 m.

The area of the pond is 19.5 acres, or eight hectares. At low tide the mean depth is 0.54 m. and the volume about 42,000 m^3; on the mean high tide the mean depth is 0.75 m. and the volume about 59,000 m^3. Thus the water lost from the pond following a mean high tide is 30% of the high tide volume. At spring tides this proportion may be as high as 65%; during neap tides it is reduced to zero. Although a thorough hydrographic study was not attempted, a number of observations indicated that the flood tide water generally

Figure 3. Northwest arm of Little Harbor.

tended to move in at all levels, pushing the old water back, so that the degree of mixing and exchange in the upper arms of the pond was not as great as the above figures would imply.

The two fresh-water streams which empty into the pond are both tidal, and at low tide the volume of water entering the pond from each of these is represented by a very slow-moving stream of about 1 ft² in cross-section. Thus the volume of water which they contribute to the pond is negligible as compared with that which enters with the tide. The bottom of the pond is covered for the most part with a thick layer of fine black mud which supports a heavy growth of Widgeon Grass (*Ruppia maritima*).

Temperatures, salinity and hydrogen-ion concentration were measured at least twice weekly from March to September 1946 and from March to September 1947, and at longer intervals from September 1946 to March 1947. The pond was covered with ice from mid-December to mid-February. Spring and summer temperatures were quite similar in 1946 and 1947 (Table I).

TABLE I. Seasonal Variations in Morning Surface Temperatures (in °C.)

	March–April			*May–June*			*July–Sept.*		
St.	*Mean*	*Min.*	*Max.*	*Mean*	*Min.*	*Max.*	*Mean*	*Min.*	*Max.*
					1946				
A	10.0	6.5	14.0	15.5	10.3	19.4	21.6	16.1	26.2
E	9.7	6.0	15.0	16.4	11.6	19.2	21.9	16.9	26.4
K	9.9	6.4	14.5	16.0	12.6	19.8	21.1	16.8	25.8
					1947				
A	9.2	3.5	17.1	15.2	7.4	27.8	23.8	20.5	27.6
E	9.8	3.1	17.5	15.6	7.3	29.8	24.6	20.5	28.3
K	8.0	3.3	15.2	15.2	7.1	26.1	23.3	20.9	26.8

Between March and September (both years) there were no marked seasonal variations in the salinity, which fluctuated irregularly depending upon the amount of rainfall and the rate of evaporation. The normal range of this variation was 26.00 to 36.00 °/₀₀, rarely dropping to 20.00 °/₀₀ or slightly lower, and occasionally rising to nearly 40.00 °/₀₀.

At Station K, near the dam, the pH generally ranged between 7.8 and 8.2 with little perceptible seasonal change. In the upper arms of the pond the pH range was considerably wider, most readings falling between 7.8 and 8.6 with extremes of 7.1 and 9.1. From July through September the pH averaged about 0.5 unit higher than in the spring months.

In a study of the biological productivity of an aquatic area, obviously the quality as well as the quantity of the phytoplankton produced is an important consideration. Aside from the question of

noxious species such as those responsible for "red water," the different phytoplankton species doubtless vary in their nutritive value for the herbivores subsisting upon them, both in respect to chemical composition and to cell size. In our present state of ignorance regarding comparative nutritive values, a mere listing (Table II) of the plank-

TABLE II.—Photosynthetic Organisms Identified from the Pond, 1946 and 1947. (Numbers in parentheses indicate the order of frequency in which organisms occurred in the samples, e. g. *Navicula* was identified from a greater number of samples than was any other genus.)

Diatoms	Diatoms—Cont.	Flagellates	Chlorophyceae
Amphiprora (6)	*Distephanum*	*Eutreptia* (7)	*Carteria*
Chaetoceros (10)	*Fragillaria*	*Exuviella* (5)	*Pyramimonas*
Navicula (1)	*Guinardia*	*Peridinium* (2)	*Scenedesmus*
Nitzschia (3)	*Gyrosigma*	*Prorocentrum* (8)	
Pleurosigma (4)	*Lichmophora*	*Ceratium*	Xanthophyceae
Skeletonema (9)	*Melosira*	*Ebria*	*Olisthodiscus*
Amphora	*Paralia*	*Euglena*	
Asterionella	*Rhizosolenia*	*Hymenomonas*	
Biddulphia	*Striatella*	*Kephyrion*	
Cocconeis	*Surirella*	*Lepocinclis*	
Coscinodiscus	*Thalassiosira*	*Mallomonas*	
Cyclotella	*Thalassiothrix*	*Ochromonas*	

tonic algae and colored flagellates identified from the pond will suffice for the purpose of this report. The ten genera most often represented are numbered in the order of the frequency of their occurrence in the samples.

In neither year was an early spring flowering observed, although it is possible that undetected blooms occurred before frequent sampling was begun in mid-March. In terms of volumes and chlorophyll concentrations, minor blooms occurred in April, May and June, but in both years the major blooms came in August and early September. *Peridinium* contributed usually four-fifths or more of the total cell volume in these latter blooms. In terms of volume this genus was the most important single fraction of the population throughout the year, except in the late spring blooms when it was largely replaced by small unidentified flagellates.

EXPERIMENTS

Six experiments, differing in design as to types of fertilizers used and number of applications, were conducted during the two years' work. Fertilizers were applied only during periods when the tidal exchange was small. The method of fertilizing consisted in broadcasting commercial fertilizers from a boat which was being rowed about in that part of the eastern arm of the pond which is north of the dotted line in Fig. 2. This section was designated the "fertiliza-

tion area." In the 1947 experiments, following each application, the boat was rowed about for half an hour to aid in the distribution of the fertilizers. The extreme northern part of the pond, represented by Station A, was termed the "control area." The nitrate fertilizers dissolved readily, whereas the superphosphate apparently sank to the bottom and went into solution slowly. The amounts and ratios in which the fertilizers were used were determined by various theoretical and practical considerations, and by the dictates of experience as the work progressed. It seemed desirable to increase the nutrient concentrations to values well above the maxima found in the sea (about 3 μg.-at. PO_4 P and 43 μg.-at. NO_3 N per liter; Sverdrup, Johnson and Fleming, 1942), while it was neither feasible nor desirable to approximate the concentrations employed in culture media for marine diatoms, such as 56 μg.-at. P and 1,100 μg.-at. N per liter in Ketchum and Redfield's (1938) modification of Miquel's solution. When nitrate and phosphate were applied simultaneously they were added in proportions intended to yield nitrate nitrogen and phosphate phosphorus in solution in the 16 : 1 atomic ratio in which they are taken up, on the average, in the open ocean (Sverdrup, Johnson and Fleming, 1942). It should be added, however, that the prefertilization ratio in the pond water varied between 0.48 : 1 and 45 : 1; the mean ratio was only 7.8 : 1.

In Table III the experiments are listed and briefly described. The last column of the table gives, for each application, the calculated increase in concentration of nutrients which theoretically should have resulted from that application.

A. Effects of Added Fertilizers upon Phosphate and Nitrate Content of the Water

1. Immediate Effect

a. *Phosphate.* In the five experiments in which superphosphate was used, the initial application theoretically should have increased the phosphate phosphorus concentration in the fertilization area by 25 μg.-at./l. Prior to the first application of fertilizers, the mean concentration in that area had been 0.38 μg.-at./l. The highest values recorded following initial applications occurred between one and seven hours after fertilizing. In these experiments the mean increase in the fertilization area ranged from 3.0 to 11.2 μg.-at./l.; the grand average of increase was 7.1 μg.-at./l. Since the pond was fertilized only during periods of reduced tidal exchange, the difference between theoretical and observed values cannot be attributed to tidal action. The probable explanation for this difference is that the

TABLE III.—Summary of Fertilizations by Date, Fertilizers Added, and Theoretical Increases of P and N Concentrations in the Fertilization Area

Expt.	*Date*	*Fertilizers Added*	*Theoretical Increases (see text)*
	1946		
1	Aug. 13	71 lbs. 20% superphosphate	25 μg.-at. PO_4P/l.
2	Aug. 26	132 lbs. NH_4NO_3	194 μg.-at. NO_3N/l.
3	Sept. 2	71 lbs. 20% superphosphate	25 μg.-at. PO_4P/l. and
		71 lbs. NH_4NO_3	194 μg.-at. NO_3N/l.
		61 lbs. $NaNO_3$	
	1947		
4	Apr. 28	30 lbs. 47% superphosphate	25 μg.-at. PO_4P/l.
	Apr. 30	15 lbs. 47% superphosphate	12.5 μg.-at. PO_4P/l.
	May 2	ditto	ditto
	May 5	ditto	ditto
	May 7	ditto	ditto
	May 9	ditto	ditto
5	July 21	30 lbs. 47% superphosphate	25 μg.-at. PO_4P/l. and
		54 lbs. $NaNO_3$	80 μg.-at. NO_3N/l.
	July 23	15 lbs. 47% superphosphate	12.5 μg.-at. PO_4P/l. and
		54 lbs. $NaNO_3$	80 μg.-at. NO_3N/l.
	July 25	ditto	ditto
	July 28	ditto	ditto
	July 30	ditto	ditto
	Aug. 1	ditto	ditto
	Aug. 4	54 lbs. $NaNO_3$	80 μg.-at. NO_3N/l.
	Aug. 6	ditto	ditto
6	Aug. 22	30 lbs. 47% superphosphate	25 μg.-at. PO_4P/l. and
		54 lbs. $NaNO_3$	80 μg.-at. NO_3N/l.
	Aug. 25	15 lbs. 47% superphosphate	12.5 μg.-at. PO_4P/l. and
		54 lbs. $NaNO_3$	80 μg.-at. NO_3N/l.
	Aug. 27	ditto	ditto
	Aug. 29	ditto	ditto
	Sept. 1	ditto	ditto

phosphate did not dissolve immediately from the fertilizer, although it is also possible that it went into solution only to be absorbed immediately on the bottom or taken up by the phytoplankton. These three possible explanations are not mutually exclusive, but the experience of Gross, *et al.* (1946) would seem to favor the first. Following their fertilization of Caol Scotnish with undissolved superphosphate (the technique employed at Cohasset), they estimated that not more than one-fourth of the phosphate in the fertilizer dissolved immediately at fertilization, but that some of the phosphate which sank to the bottom went into solution later. However, when these same investigators dissolved the superphosphate before applying it to Loch Craiglin, they detected much higher proportions of the theoretically expected values; indeed some of their readings exceeded the theoretical (Orr, 1947).

b. *Nitrate.* Nitrate was not measured in Experiments 2 and 3.

As will be seen below, however, the repeated application of nitrate (Experiments 5 and 6) had no cumulative effect upon its concentration in the open water. Therefore, each application in these experiments had an effect comparable to a single fertilization. The mean value for the fertilization area prior to Experiment 5 had been 3.4 μg.-at. NO_3N/l. In the 13 applications in Experiments 5 and 6, the average increase in concentration two hours later ranged from 24.6 to 123 μg.-at. N/l.; the grand average of increase was 80.5, which was the theoretically predicted increase. These results are comparable to those reported by Orr (1947). Thus the correspondence of the actual to the theoretical increase in nitrate concentration was, albeit irregular, closer than in the case of phosphate. This no doubt reflects the greater solubility of the nitrate fertilizer.

2. Duration of Effect

a. *Phosphate.* Because of the obvious risks in fertilizing a body of water subject to any degree of tidal exchange, the duration of the effects of fertilization is of great practical importance. Let us consider first the fate of added phosphorus following single applications of fertilizers. This was studied in Experiments 1 and 3 (Fig. 4). The time of fertilization is indicated by an arrow on the baseline. In each of these experiments the resulting phosphate maxima at the two stations within the fertilization area (D and E) differed widely; doubtless this was the result of imperfect distribution of the fertilizer. In both experiments phosphate at the various stations was affected in the order of their proximity to the fertilization area, in regard to both the intensity of the effect and its immediacy. At the control station (A), phosphate values during these experiments remained well within the limits observed prior to fertilization.

In Experiment 1, the effect of fertilization upon the phosphate content of the water lasted only one day; in Experiment 3 it lasted about one week. This difference cannot be laid to a difference in the rate of phosphate absorption by the phytoplankton, since the amounts of plankton present in the fertilization area during these experiments were very nearly identical. Moreover, in Experiment 3 the presence of added nitrate should have allowed a greater rate of phosphate absorption by the phytoplankton, for it is known that the rate of phosphate absorption depends upon the nitrate as well as the phosphate concentration (Ketchum, 1939a). Possibly the more rapid disappearance of phosphate from the water in the first experiment was due to a greater degree of adsorption by the bottom. The mud was thus saturated to the extent that when phosphate was again

applied 20 days later (Experiment 3) a greater amount of it remained in solution until removed by other agencies.

The increased phosphate concentrations resulting from single applications of superphosphate to Loch Craiglin by Gross and his coworkers usually lasted less than a week (Orr, 1947). In most of the experiments described in detail, added phosphate had largely disappeared in three or four days, although in the only experiment thus described which produced nutrient concentrations as great as those

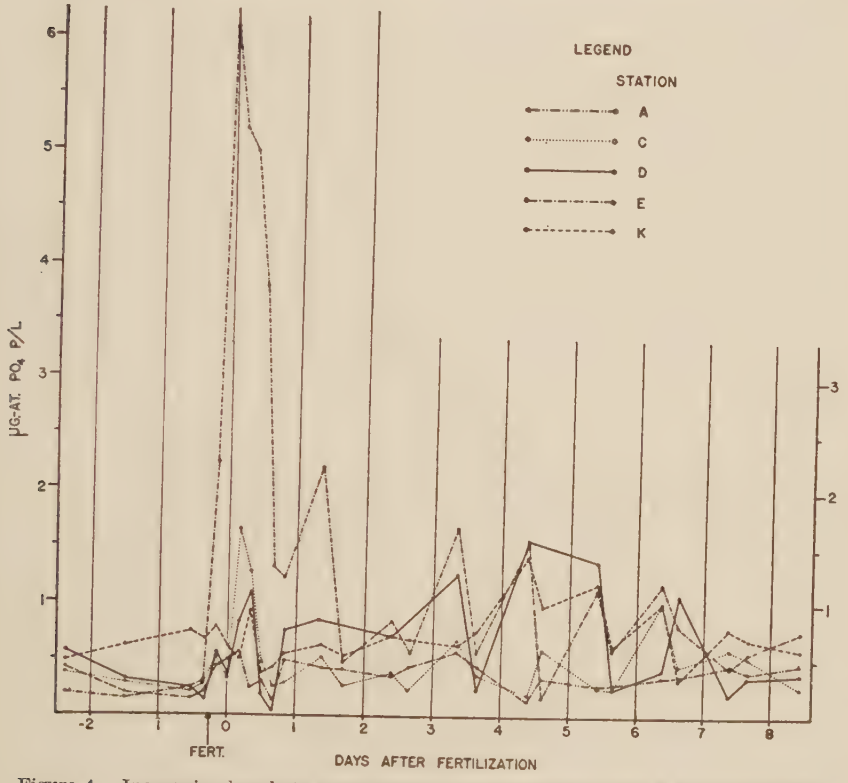

Figure 4. Inorganic phosphate concentration in the water following a single application of superphosphate fertilizer (Experiment 3).

produced at Cohasset, appreciable quantities of the added phosphate were detected about a week after fertilizing but had disappeared at the end of another week.

After applying the fertilizers in Experiment 3, phosphate readings were taken at least twice daily at about 9:30 a. m. and 3:30 p. m.

The vertical guide-lines in Fig. 4, spaced at 24-hour intervals, indicate midnight. It is evident that, following the fertilization, there was a diurnal fluctuation in phosphate values, with high readings in the morning and low readings in the afternoon. This was especially pronounced and persistent at the stations in the fertilization area, although at Station D the effect was somewhat obscured by the fact that on three afternoons the water level at this station was so low that it was impossible to get a sample. The degree of fluctuation can be expressed quantitatively as the ratio of the morning reading to the afternoon reading of the same day. The mean of these ratios for each station then provides a basis for comparison between stations. Expressed as factors, these averages are as follows: Station D, 7×; E, 3×; C, 1.5×; K, 1.3×. At Station A in the control area the factor is − 0.07×, indicating no significant fluctuation whatever. Thus the degree of fluctuation is consistently correlated with proximity to the fertilization area.

Newcombe (1940) has reported a somewhat similar diurnal phosphate pulse in the (unfertilized) waters of the Chesapeake Bay. The diurnal differences which he observed were of the order of 0.5 μg.-at. P/l., or about one-half as great as the diurnal differences discussed above. To account for this fluctuation Newcombe postulated a diurnal change in the phosphate metabolism of the phytoplankton, wherein phosphate is supposed to be released in large quantities by the plants during the night and reabsorbed during the day.

Since in the present work the diurnal pulse was correlated with proximity to the fertilization area, the facts here reported can be explained more easily on a different basis. It is suggested that the phosphate in the fertilizer, rather than dissolving immediately and all at one time, went into solution gradually over a period of several days. Presumably this occurred at a rate independent of the light intensity. While it is not known whether the phytoplankton was phosphorus deficient before the fertilization, Ketchum (1939b) has shown that only phosphorus deficient cells will take up phosphate in the dark, and his data make it seem nearly certain that if such a deficiency existed it would have been restored during the first day after fertilization. Assuming, then, no phosphorus deficiency after the fertilization, the more or less constant rate of solution of the fertilizer would allow a high phosphate concentration to accumulate during the hours of darkness when the phytoplankton was not photosynthesizing. During the day this concentration was then reduced by the activity of the plants. If suitable data were available on the rates of phosphate absorption in laboratory cultures, one might judge whether the phytoplankton would be capable of bringing about the

daily reduction in phosphate values, as proposed in this theory. The only published information on rates of phosphorus uptake appears to be that of Ketchum (1939a). Unfortunately, his *Nitzschia closterium* cells were so much smaller than the *Peridinium* cells which formed the bulk of the pond phytoplankton that one cannot predict the rate of absorption by *Peridinium* from Ketchum's data. However, there is some evidence to support the proposed explanation of the phosphate pulse. Throughout the period in which the pulse was observed, the total phytoplankton volume at Station D was very much greater than that at Station E (Fig. 7). While the phosphate record for Station D is admittedly incomplete, in so far as it goes, it indicates a considerably greater degree of diurnal fluctuation than that observed at Station E. This correlation between phytoplankton concentration and phosphate fluctuation is in accord with the above interpretation of the phosphate pulse.

However, in comparing Station E with the station in the control area one finds a negative correlation between phytoplankton concentration and phosphate pulse. At Station E phytoplankton volume was low and phosphate fluctuated greatly; at Station A the phytoplankton concentration was many times greater, yet no phosphate pulse was observed. This is explained by the much higher phosphate concentrations at Station E, which should increase the rate of phosphate absorption by the phytoplankton (Ketchum, 1939a).

If the phosphate pulse in the fertilization area results from the interaction of continuous supply and discontinuous consumption, the normal regeneration of phosphate in the control area and its absorption by the phytoplankton might be expected to produce a diurnal pulse of greatly reduced amplitude. That no pulse was observed indicates that either the amounts of phosphate regenerated nightly and absorbed daily were too small to produce a detectable diurnal variation, or that the phytoplankton, known to be extremely dense, was phosphorus deficient and therefore absorbed phosphate by night as well as by day.

In view of the rapid disappearance of phosphate following single applications, in the second year's experiments (Nos. 4, 5 and 6) the attempt was made to maintain nutrient levels of the order of 5 μg.-at. P/l. and (in the last two experiments) 80 μg.-at. N/l. by the repeated application of fertilizers. The results of Experiments 4 and 5 are shown in Figs. 5 and 6. Fertilizations are indicated by arrows, and for the sake of clarity the readings at Stations E, P and Q in the fertilization area have been averaged. Except in Experiment 4, the area represented by Station A appears to have served as a fairly

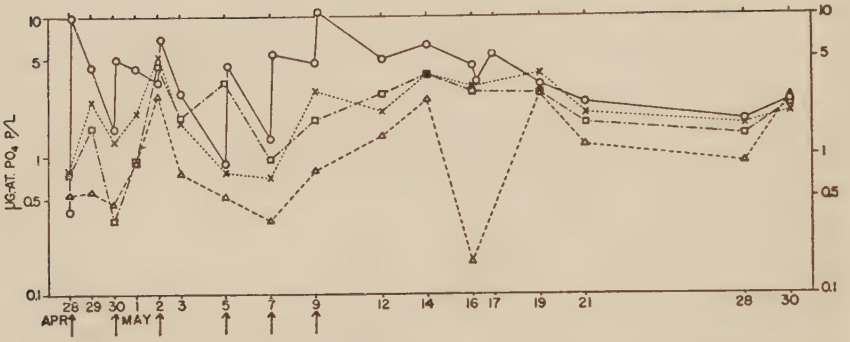

Figure 5. Inorganic phosphate concentration in the water during and following the repeated application of superphosphate fertilizer (Experiment 4). Arrows at bottom of figure indicate applications of fertilizer. Squares = Station K, triangles = Station A, X's = Station C, circles = mean of Stations E, P and Q.

effective control, in that the fertilizations influenced only slightly the nutrient concentrations in that area.

Experiment 6 was cut short by an unusually heavy rain on September 2 which lowered the salinity from about 34 °/₀₀ to values ranging from 7 to 16 °/₀₀ on September 3. Since the phytoplankton (chiefly *Peridinium*) was almost completely wiped out, it was decided to terminate the experiment.

In Experiments 4 and 5 a cumulative effect of repeated fertilizations upon phosphate values was clearly evident. Following the last application in Experiment 4, concentrations remained substantially above 1 μg.-at. P/l. at all stations for six weeks; in Experiment 5 the concentration in the fertilization area remained above that level for two weeks after the last application. This effect is believed to be due to the accumulation of phosphate reserves in the mud which were then given off gradually.

The more rapid disappearance of phosphate in Experiment 5 (also Experiment 6, not figured) than in Experiment 4 is probably related to its rate of absorption by the phytoplankton. Not only was the phytoplankton population denser in Experiments 5 and 6 than in Experiment 4 but, for three reasons, it seems likely that the *net* rate of assimilation was higher in these later experiments: 1) for the most part the weather was clear, whereas during Experiment 4 it had been consistently overcast; 2) the mean temperature was approximately 10° higher; and 3) the presence of added nitrate (lacking in Experiment 4) should have further stimulated photosynthesis and phosphate assimilation.

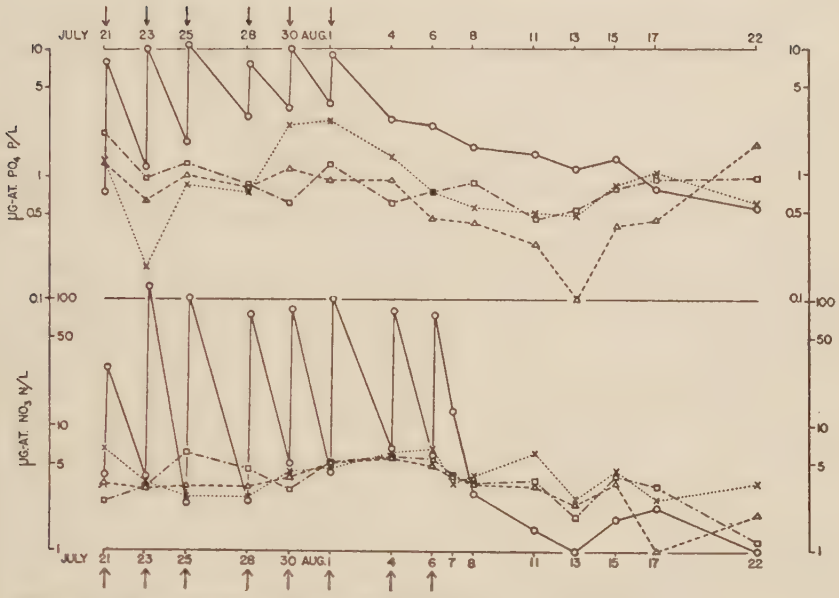

Figure 6. Concentrations of inorganic phosphate and nitrate during and following the repeated application of superphosphate and sodium nitrate fertilizers (Experiment 5). Arrows at top of figure indicate applications of superphosphate; arrows at bottom indicate nitrate applications. Squares = Station K, triangles = Station A, X's = Station C, circles = mean of Stations E, P and Q.

The diurnal phosphate pulse in the fertilization area was measured once in Experiment 4 (Fig. 5). Readings were made at 1 p. m. and at 4 p. m. on May 16 and again the following morning at 9, producing the sharp notch observed in the curve, which gives some idea of the magnitude of diurnal fluctuation. (The measurements on other days were made in middle or late morning, except for those following an application of fertilizers; these were made in midafternoon.)

b. *Nitrate.* The duration of effect of nitrate fertilizers upon nitrate concentrations in the water was observed in Experiments 5 and 6. Although the highly soluble sodium nitrate produced the theoretically predicted increase, it is clear from Fig. 6 that this high value could not be maintained, even when fertilizer was applied as often as eight times in 17 days. Only once was nitrate measured the day after a fertilization (Aug. 7, Fig. 6); on this occasion almost all the added nitrate had disappeared in 24 hours. The fate of this nitrate is not known. No doubt some of it was taken up by the phytoplankton, but the detection of hydrogen sulphide in the bottom mud suggests

that much of the nitrate may have undergone chemical reduction.

The distribution of added nitrate was well "controlled," in that it did not affect the concentrations at Stations A and K except toward the end of Experiment 6.

B. Effects of Added Fertilizers upon the Standing Crop of Phytoplankton

It is to be expected that the size of the phytoplankton standing crop may vary seasonally over a wide range, and that occasional blooms occur "spontaneously," *i. e.*, in the absence of artificially added nutrients. For this reason, and because in our present state of knowledge it cannot be assumed that all the effects of increased nutrient concentrations will be manifest immediately, it is necessary to coordinate in a single view the events of an entire season, in order to assess the effects of the experiments upon the phytoplankton. Phosphate concentration and phytoplankton volume (converted and expressed as chlorophyll *a*) at the stations in the fertilization area and at Stations A and K for March–September 1946 are shown in Fig. 7. For 1947 the variations in nitrate as well as phosphate are given in relation to the direct measurement of chlorophyll *a* (Fig. 8).

The central aim of the first year's experiments was to obtain information on the rate of phosphate disappearance. The repeated application of fertilizers was not attempted in 1946, and the response of the phytoplankton to single applications need not be discussed at any length. In the experiment involving a single application of phos-

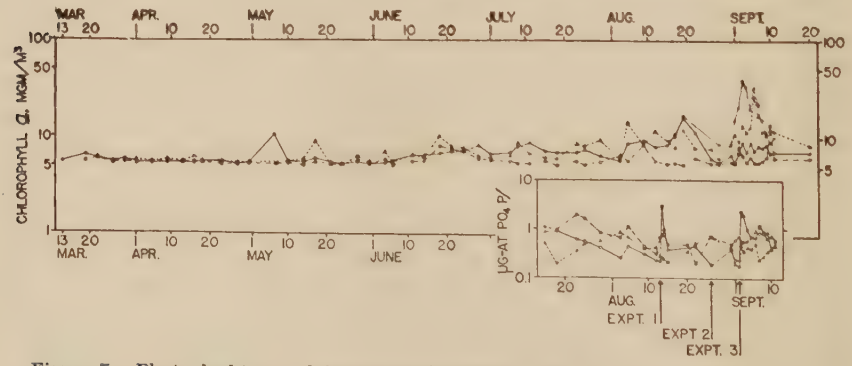

Figure 7. Phytoplankton and inorganic phosphate, 1946.

Squares = Station K; triangles = Station A; X's = Station D; Circles = phytoplankton for Station E and phosphate for fertilization area (Station E, July 15–August 13; mean of Stations E and D, Aug. 14–Sept. 11). Chlorophyll values computed from total cell volumes (see p. 39). Phosphate record Aug. 12–15 and Sept. 2–10 as daily averages only (for details of latter dates, see Fig. 4). The beginning of each experiment is indicated by an arrow at bottom of figure.

phate only (Experiment 1), the highest phytoplankton values observed at Station E in 1946 occurred six days after the fertilization. Values for Station D, also in the fertilization area, were in close agreement. However, a moderate flowering had started in the control area (Station A) a week prior to the experiment. It is quite possible, therefore, that the bloom in the fertilization area originated from causes affecting both arms of the pond and was independent of the fertilization. Six days after the single application of nitrate (Experiment 2), an intense but very local bloom developed in the vicinity of Station D and lasted one week. Station E was not affected, and again a presumably spontaneous bloom occurred in the control area. The single application of phosphate and nitrate (Experiment 3), which produced rather high phosphate values for one week in the fertilization area and at Station K, apparently had no effect upon the phytoplankton of the fertilization area, but may have produced the ephemeral flowering at Station K eight days later.

The 1947 experiments, involving the repeated application of fertilizers, were designed to show the effects upon the phytoplankton of nutrient concentrations maintained at high levels. The repeated applications of phosphate alone (Experiment 4) were made during a

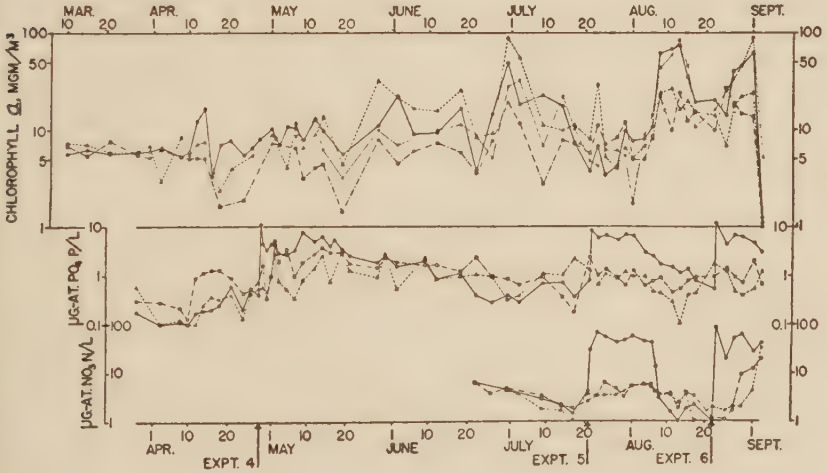

Figure 8. Phytoplankton, inorganic phosphate and nitrate, 1947.

Squares = Station K; triangles = Station A; X's = Station P; circles = phytoplankton for Station E; phosphate for fertilization area (Station E until April 26, mean of Stations E, P and Q thereafter). Chlorophyll values: for March computed from total cell volumes, thereafter measured directly. Phosphate record April 30–May 16, and phosphate and nitrate July 23–Aug. 6 and Aug. 25–Sept. 1 as daily averages only (for details see Figs. 5 and 6). The beginning of each experiment is indicated by an arrow at bottom of figure.

period of consistently cloudy weather and had no immediate influence on the size of the standing crop. It should be noted that during and particularly following this series of fertilizations, phosphate reached high values in all parts of the pond, and had hardly returned to the early spring level (approximately 0.5 μg.-at. P/l.) when Experiment 5 was started on July 21. In the first half of June there was some increase in phytoplankton at Station E and a more sustained bloom at Station A, which in this experiment did not serve as a control. At the end of June the flowering spread to all areas and attained roughly twice the magnitude of the 1946 maximum. If the increased phosphates resulting from Experiment 4 played any part in this June blooming, other factors (*e. g.* light) must have been equally important, since the bloom did not start until one month after the beginning of the experiment.

The repeated applications of phosphate and nitrate in Experiment 5 affected nutrient concentrations in the fertilization area only. A very heavy bloom developed there, starting 16 days after the beginning of the experiment. At the same time the populations at Stations A and K increased to about one-third the density in the fertilization area. The distribution of phytoplankton was then equalized again, at a rather high concentration, by the high tides of August 11–21.

When the same fertilizers were again added in Experiment 6, the phytoplankton at Stations A and K continued to oscillate about the same general level, while that in the fertilization area immediately began to bloom heavily and reached the same density attained in Experiment 5. The experiment was cut short on the thirteenth day (September 3) when virtually all phytoplankton, as judged by chlorophyll analyses, had disappeared from the surface layers as a result of the rainstorm of the previous day.

DISCUSSION

The widespread flowering one month after the beginning of Experiment 4 and the bloom in the fertilization area 16 days after the start of Experiment 5 suggest the possibility of a delayed effect of fertilization upon the growth of the phytoplankton. An "initial lag" period preceding the increase in standing crop is a phenomenon of population growth among unicellular organisms that is as well known as it is poorly understood. Phelps (1935) demonstrated such a lag in laboratory populations of the ciliate *Glaucoma pyriformis* and compared it with the lag long known to occur in bacterial cultures. Riley (1943) observed the same phenomenon in mixed diatom populations taken directly from the sea, and a lag lasting up to 15 days in the growth of some of his *Nitzschia closterium* cultures in sea water en-

riched with commercial fertilizers. He interprets the relatively high proportion of senile cells and high rates of respiration and photosynthesis during the lag in his *Nitzschia* cultures as indicating that the lag is a period of rapid growth and rapid death. The delayed blooming of fertilized fresh-water ponds is a problem familiar to fisheries workers. According to Swingle (1947), the experimental ponds at Auburn, Alabama, normally bloom within one to three days after fertilizing with nitrogen, phosphorus, and potassium, but in some cases the flowering is delayed for as long as one month.. During such a lag the plankton did not respond to any of a variety of treatments, including artificial aeration of the water, inoculation with actively growing algae, addition of minor nutrient elements (zinc, manganese, iron, iodine, boron and copper) and addition of vitamins B_1 and B_6. Swingle attributes the lag in some cases to organic bottom deposits, with whose associated bacterial flora the autotrophic plankton could not compete for inorganic nutrients; other cases he assigns to a lack of sufficient carbon dioxide. It does not seem likely that either of these proposed explanations could be applied to the "delayed" blooms here described. Swingle's first hypothesis requires that the added nutrients be almost entirely consumed by the bacteria, whereas in the present experiments an abundant supply of dissolved phosphate remained throughout the "lag" periods. The great excess of bicarbonate present in sea water and the undetermined but presumably high rate of carbon dioxide evolution from decomposing organic deposits would seem to preclude the possibility of a carbon dioxide shortage.

The question naturally arises as to whether the eventual flowering of a fertilized pond, following a lag, is or is not related to the fertilization. The magnitude of the growth which follows a lag in laboratory cultures, such as Riley's *Nitzschia*, is a function of the nutrient concentration at the start of the experiment, and it is implicit in Swingle's report on fertilized ponds that the bloom following even a month's lag is related to the fertilization in the same manner. This implication must depend upon the observation that the delayed bloom is greater (in intensity, duration, or both) than spontaneous blooms occurring in unfertilized ponds. This comparison would appear to provide the only standard of judging whether a delayed bloom owes its magnitude to the fertilization. Applying this criterion to the "delayed" blooms in the Cohasset pond (June and early August 1947), one notes that the first of these endured much longer than any previous bloom and that both reached maxima two times as great as had been observed before. Therefore it seems quite probable that the fertilizations of Experiments 4 and 5, respectively, were

responsible for the magnitude of these blooms. The June flowering may well have been delayed, at least in part, by the lack of sufficient sunlight during the cloudy month of May. To explain the 16 day lag in Experiment 5 we must look to other causes, for the weather was clear throughout this period. It seems likely that some undetected environmental factor affecting the entire pond was unfavorable during this interval; a change in this factor then permitted a moderate amount of growth at Stations A and K and a dense bloom in the area rich in phosphorus and nitrogen.

A discussion of the immediate and delayed results of individual experiments does not exhaust all the possible effects of fertilization upon the standing crop of phytoplankton. Figs. 7 and 8 considered together show that, in so far as the conversion of volumetric data into chlorophyll equivalents is reliable, the average standing crop was appreciably greater after May 1947 than before. It is possible that this increase was quite independent of our manipulations, but the enrichment of the entire pond with phosphate resulting from the May fertilizations strongly suggests a cumulative effect of at least the last three experiments upon the growth of the phytoplankton.

To summarize regarding the effects of fertilization upon the phytoplankton, the results of the first three experiments do not permit any conclusions, Experiments 4 and 5 may have produced more or less delayed effects, Experiment 6 was followed by an immediate increase, and the second season's fertilizations collectively appear to have raised the general level of phytoplankton abundance for the entire summer. These results are quite similar to those obtained in the Loch Craiglin investigations (Marshall, 1947), which involved eleven fertilizations between August 1942 and March 1944. There is good evidence that three of these (Dec. 30, 1942, Sept. 1 and Nov. 5, 1943) produced immediate increases in the nannoplankton (although not in the diatoms or dinoflagellates), and the last three fertilizations appear to have had somewhat delayed but more lasting effects upon the diatoms and especially the dinoflagellates. The latter were more abundant in 1943 than in 1942 and increased further in 1944, apparently showing a cumulative effect of the successive fertilizations.

A sustained increase in the phytoplankton standing crop, such as is suggested in both the Cohasset and Loch Craiglin studies, would doubtless accelerate the productivity of the area at all trophic levels more effectively than would the same total production of phytoplankton apportioned in alternating periods of abundance and scarcity. This is the basis, in fresh-water fish-pond management, for the practice of applying fertilizers in small amounts at frequent intervals (Swingle and Smith, 1938). Some idea of the possible duration of

fertilization effects is gained from the experience of Einsele (1941). Superphosphate fertilizations of a fresh-water lake in the summer of 1938 produced, in the summer of 1939, total phosphorus and phytoplankton concentrations considerably greater than those found in the years prior to 1938.

In general, the rate of disappearance of added phosphate in the Cohasset experiments appears to have been a function of the abundance of phytoplankton. Note the acceleration of its disappearance with the plankton increase at the end of June 1947 and its much more rapid decrease during Experiment 5 than in Experiment 4. Furthermore, the densest phytoplankton populations coincided with, or followed closely upon, periods of maximum phosphate concentration, and the combined effects of the last three experiments appear to have brought about a long-term increase in the standing crop.

SUMMARY

1. The application of commercial superphosphate fertilizers to a salt water pond partially cut off from the sea raised the phosphate content of the water by approximately one-third of the theoretically calculated increase. Phosphate concentrations several times as high as the prefertilization values were maintained for several weeks by the addition of superphosphate in six applications over a period of two weeks.

2. Following an application of superphosphate, phosphate concentration in the area fertilized exhibits a diurnal pulse, which is believed to result from the continuous solution (day and night) of the fertilizer phosphate combined with a discontinuous absorption (in the daylight hours only) by the phytoplankton.

3. The application of commercial sodium nitrate raised the nitrate concentration of the water by the theoretically calculated increase. However, nitrate concentrations could not be maintained above the prefertilization values for more than 24 hours, even by the repeated application of sodium nitrate every second day.

4. The artificially increased concentrations of phosphate and nitrate resulted in increases in the standing crop of phytoplankton to several times the prefertilization maximum. This effect was realized within a few days, or after an initial lag of two to four weeks. The several fertilization experiments collectively appear to have produced a significant increase in the standing crop which lasted throughout the second summer of fertilizing.

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THEORETICAL ANALYSIS OF SEASONAL CHANGES IN THE PHYTOPLANKTON OF HUSAN HARBOR, KOREA

By

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INTRODUCTION

It has been shown (Riley, 1946, 1947) that seasonal changes in total phytoplankton populations can be depicted with a reasonable degree of accuracy by a simple theoretical construction in which the rate of change of the population is described in terms of physiological processes that increase or decrease its organic content (photosynthesis, respiration, grazing), and in which the rates of the individual processes are quantitatively predictable by reference to a few environmental factors. In the papers cited, an examination was made of the seasonal cycles of phytoplankton in the Georges Bank area of the Gulf of Maine and in coastal waters south of New England. The cycles were markedly different, but the same equation was applicable in each case, suggesting that variations in the cycles were attributable to simple environmental differences in the two areas.

These papers fall far short of a definitive treatment of the problems of plankton variation. The general principles appear to be sound, but the details of the application are greatly over-simplified. Improvements in method will require more complete laboratory and field data, but the success of these future investigations will be more secure if the problems are further clarified by continuing the examination of existing data. One phase of the problem that has been studied recently is the regional distribution of plankton (Riley, Stommel and Bumpus, 1949). Another phase, to be investigated here, is the ecological basis for differences that occur in plankton cycles from one year to the next. The chief requirement for such a study is a very complete set of data on both the plankton and its environment. A survey of Husan Harbor, Korea, was found to be particularly suitable for the purpose.

MATERIAL

A survey of the neritic plankton of Japanese waters was summarized by Kokubo (1940) and published more extensively (in Japanese)

[1] Contribution No. 472 from the Woods Hole Oceanographic Institution.

in a series of papers in the *Plankton Journal.* The survey was sponsored by the National Research Council of Japan on the recommendation of a conference of some of the leading marine biologists of that country. H. Marukawa, F. Fugita, S. Suzuki, and other investigators cooperated with Kokubo in a program resulting in the collection and examination of some 450 samples at 16 stations lying between 25° and 47° North and covering the period from 1931 to 1933. Collections consisted of 10 l. of surface water taken approximately one mile off shore, usually with accompanying data on temperature, specific gravity, transparency, and water color. The collections were allowed to stand 24 hours after preservation with formalin, and the volume of sediment and numbers of organisms were then determined.

Fig. 1 shows Kokubo's observations in Husan Harbor. They were ably supplemented by a survey conducted by the Imperial Fisheries Experiment Station of Korea during 1932 and 1933, the results of which were published in tabular form in the annual reports of that

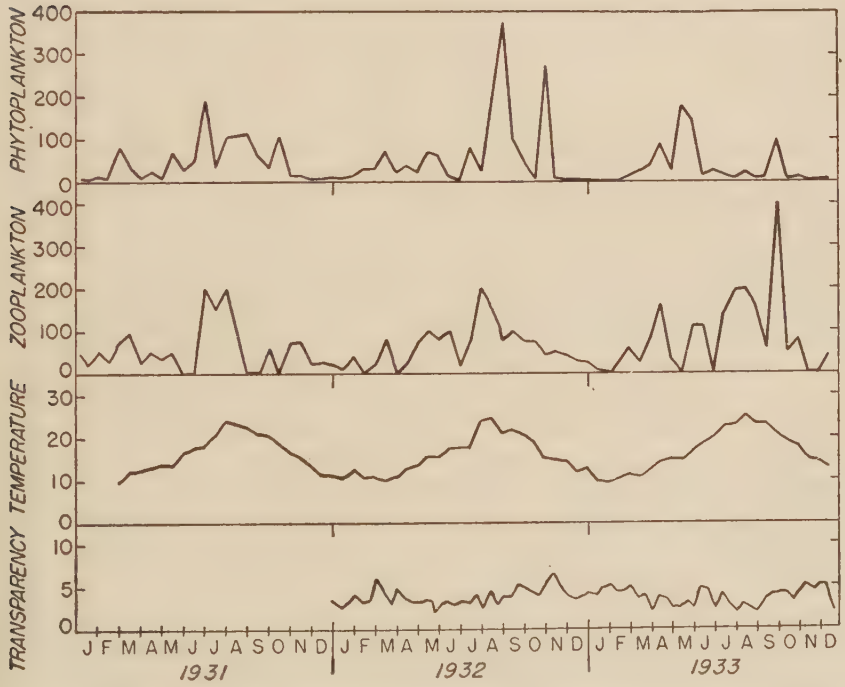

Figure 1. Seasonal cycles in Husan Harbor, Korea. Phytoplankton, thousands of cells per liter; zooplankton, number of organisms per liter; temperature, degrees Centigrade; transparency, Secchi disc reading in meters (Kokubo, 1940).

institution. Their data on nutrient salts and hours of sunshine per month, reproduced in Fig. 2, will form an important part of the analysis.

QUALITATIVE DISCUSSION

The phytoplankton data in Fig. 1 show rather large differences from one year to the next in the relative magnitude of spring and summer-autumn flowerings, the size and duration of the flowerings, and the degree of depletion following them. Differences are also apparent in zooplankton and in physical and chemical factors of the environment. Inspection of the data reveals some slight evidence of causality in these variations. The zooplankton curve suggests an inverse relation between the size and duration of the summer maximum in zooplankton and the size of the summer-autumn phyto-

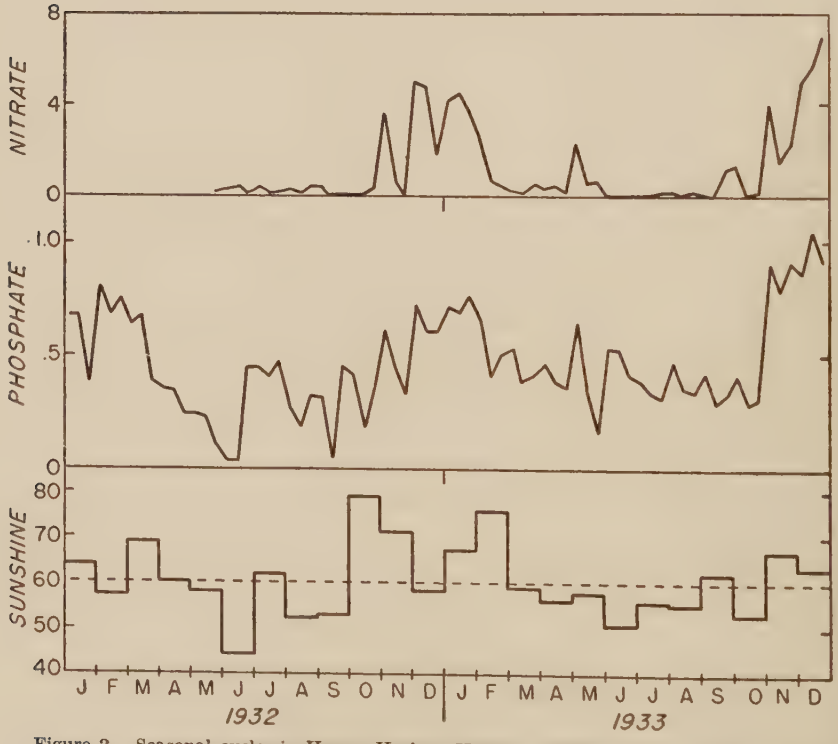

Figure 2. Seasonal cycles in Husan Harbor, Korea. Milligram-atoms of nitrate-N and phosphate-P per m³; number of hours of sunshine per month (Annual Report of the Imperial Fisheries Experiment Station of Korea, 1932, 1933).

plankton flowering, and therefore zooplankton grazing may be important in controlling the size of the summer phytoplankton population. Comparison with Fig. 2 shows that near-depletion of phosphate and absence of nitrate were accompanied by a decline in the phytoplankton population; in 1933, when there was no phytoplankton flowering until midautumn, the nitrate concentration was considerably lower than in 1932, when there was a large summer flowering. The beginning of each summer and autumn flowering—July and October 1932 and September 1933—occurred during months when the amount of sunshine was above average.

These considerations suggest that phytoplankton variations from one year to the next might be explained reasonably in terms of environmental influences. However, the relationship seems likely to be a complicated one, involving a number of factors, so that conclusive results are not to be obtained by simple inspection.

QUANTITATIVE ANALYSIS

It will be assumed initially that the processes of increase and decrease of the phytoplankton population are accurately expressed by a simple equation

$$\frac{dP}{dt} = P(P_h - R - G) \ , \tag{1}$$

in which $\frac{dP}{dt}$, the change in the population during a unit of time, is equal to the initial population P times the sum of the coefficients of the physiological processes involved, namely photosynthesis P_h, phytoplankton respiration R, and grazing G. Furthermore, since growth of phytoplankton takes the form of a geometrical progression, an initial population P_o will change during the time interval O to t according to the formula

$$P_t = P_o e^{(P_h - R - G)t} \ , \tag{2}$$

provided the coefficients remain constant during this time, and the relation between the initial population P_o and the final one P_t is expressed by

$$ln \frac{P_t}{P_o} = P_h - R - G \ . \tag{3}$$

These equations assume that the plankton populations either remain stationary or are horizontally uniform. If lateral water movements change the populations, additional expressions must be included to account for such changes.

The equations acquire ecological significance if the physiological coefficients can be rated quantitatively according to environmental influences. It then becomes possible to set up equations predicting the population change during some small interval of time in which the environmental factors can be presumed to remain relatively constant. Comparison of the observed with the predicted population changes provides a quantitative estimate of the accuracy of the method. If it proves to be adequate, the analysis immediately reveals reasons for observed differences in population growth.

In other regions where these methods have been applied, physiological experiments provided much of the necessary information for setting up the equations. These are lacking in the present case. It will be necessary to assume that the results obtained in other areas are sufficiently general in their applicability to warrant using them as a first approximation, after which statistical procedures can be used for any modifications that seem necessary because of local peculiarities or differences in observational methods.

The environmental factors will now be examined, and an attempt will be made to combine them in such a way as to express the physiological effects as accurately as possible. Beginning with photosynthesis, it is first necessary to determine the amount of light available for plankton growth and its annual fluctuations. The sunshine data in Fig. 2 supply only a partial answer to this problem because the amount of solar energy in the sunshine varies with the season according to the altitude of the sun and also because there is a considerable amount of energy derived from sky radiation on cloudy days. Thus Fig. 3, which reproduces data on total radiation from Kimball (1928), shows a large seasonal variation that is not apparent in Fig. 2.

The solid line in Fig. 3 is a generalized curve for latitude 36° N., approximately the latitude of Husan. The broken curve is for 36° N., 131°–140° E., and therefore is more precisely applicable to Husan, taking into account local variations in humidity and cloud cover. Some of the peculiarities of this curve are reflected in Fig. 2 in the tendency toward greater than average sunshine in midwinter and a low value in June. Thus the variations in Fig. 2 are in part normal for the area and in part random variation around the norm. Furthermore, a statistical comparison of the differences in the two figures can be used to estimate roughly the variations in absolute radiation during the two-year period. Thus a least squares fit was obtained between the deviation of hours of sunshine from the average (Fig. 2) and the difference between the two curves in Fig. 3. The resulting equation stated hours of sunshine for any one month in terms of

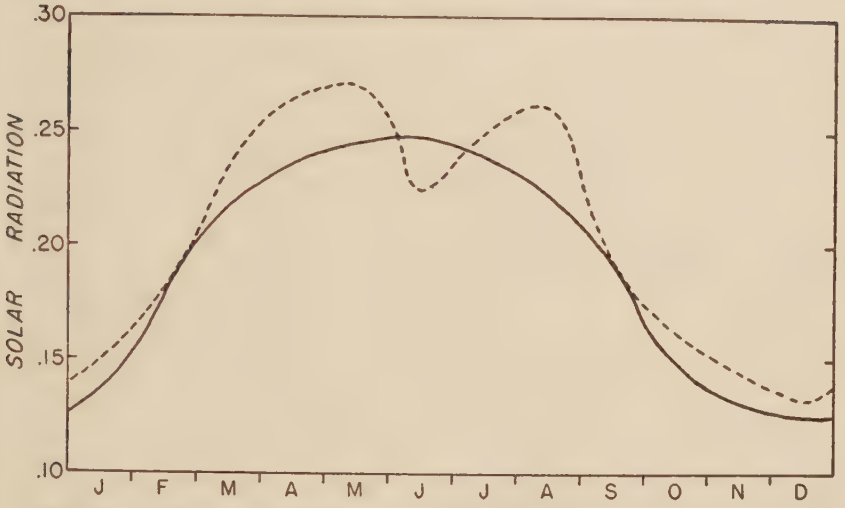

Figure 3. Incident solar radiation in g. cal. per cm² per minute. Solid line, generalized curve for Lat. 36° N.; broken line, average for 36° N., 131°–140° E.

calorific deviation from the average (solid line in Fig. 3). The estimated radiation so obtained is shown as the upper curve in Fig. 4.

Of course this is radiation at the surface of the sea. The amount obtained by the plankton at any depth depends on both the incident radiation and the transparency of the water. It is asumed at this point that the shallow water (average depth 7.7 m.) where collections were obtained was mixed thoroughly enough so that there would be no serious error in stating the effective radiation as the average light intensity in the whole water column. This is obtained by integrating the radiation from surface to bottom and dividing by the depth of water, namely

$$\bar{I} = \frac{I_o}{7.7K}\,(1 - e^{-7.7K}),$$

where I is average radiation in the whole water column in g. cal. per cm² per minute, I_o is incident solar radiation (Fig. 4), and K is the absorption coefficient, estimated as 1.7 divided by the Secchi disc reading in meters (Fig. 1). The average radiation so obtained is the solid line in the middle graph in Fig. 4.

The effectiveness with which phytoplankton uses the available radiation in photosynthesis depends in part on the availability of nutrient salts. In experimental studies of the photosynthesis and growth of pure diatom cultures and of natural populations of the

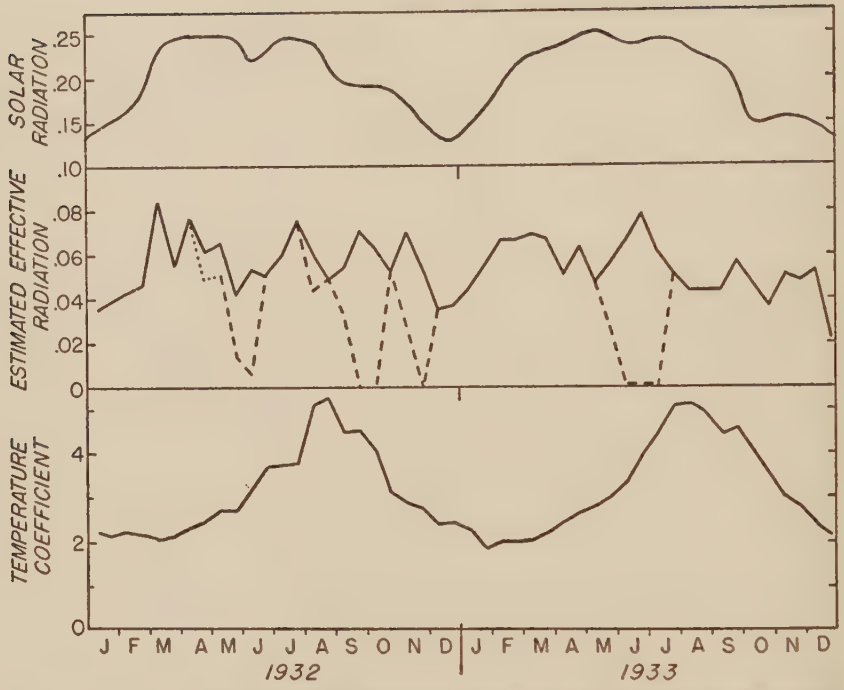

Figure 4. Upper curve, estimated incident solar radiation in g. cal. per cm² per minute; for details of calculation see text. Middle graph, solid line shows estimated average radiation in a column of water 7.7 m. deep in Husan Harbor, based on incident radiation and transparency data. Broken line shows reduction in the potential photosynthetic effect of radiation that is believed to result from depletion of nitrate or phosphate. Dotted line is a similar type of reduction estimated from phosphate alone, during a period when no nitrate data were available. Lower graph shows the relative variation in physiological rates resulting from seasonal temperature changes, on the assumption that these rates are doubled by a ten-degree increase in temperature.

western North Atlantic, it has been demonstrated that phosphate depletion has a limiting effect when the concentration falls below about 0.5 mg.-at. of P per m³ (Riley, Stommel and Bumpus, 1949). Severe nitrogen depletion also reduces photosynthesis and growth, but the quantitative relationship has not been worked out adequately. At this point, a few physiological experiments with the Husan plankton would have helped the analysis. Lacking them, it is possible only to make what seem like reasonable assumptions about nutrient effects and then test them statistically. By a process of trial and error, various combinations of assumptions about phosphate and nitrate effects were fitted into the general plankton equation (the remainder of which will be described in due course) and statistically compared

with observed plankton changes. Since the only criterion was empirical agreement, and since the whole procedure was somewhat complicated, there is no assurance that the results are entirely correct. However, they are more or less in accord with experimental data obtained elsewhere. By these methods it was found that a likely nutrient effect was: (a) a reduction of photosynthesis proportional to phosphate depletion when the latter fell below 0.3 mg.-at. of P per m^3 (for example, with a concentration of 0.15 mg.-at., the photosynthetic rate would be 50% of the maximum permitted by physical conditions prevailing at the moment); (b) reduction of photosynthesis to zero with zero nitrate concentration, but otherwise no effect. In the middle graph in Fig. 4, the broken curve shows reductions from the basic radiation curve, indicating the decrease in potential photosynthesis that results from depletion of either phosphate or nitrate. From January to May 1932 there were no nitrate observations, and reductions during this period, based on phosphate alone, are shown as a dotted line.

Temperature affects nearly every physiological process. Its simplest manifestation is an approximate doubling of the rate of any given process with a ten-degree increase in temperature, so that the rate r_T of any process at temperature T is expressed by

$$r_T = r_o\, e^{.069T} ,$$

in which r_o is the rate at 0° C. This is a great over-simplification of the real situation, but the empirical method does not permit greater refinement. The lower part of Fig. 4 shows this basic temperature effect ($e^{.069T}$), which can be used in various ways in the equation. The best statistical agreement was obtained by using the temperature coefficient as an estimate of relative changes in phytoplankton respiration and also by including it with the other factors involved in photosynthesis.[2] There was no evidence that the grazing factor was improved by postulating a temperature effect.

The net result of the investigation at this point is the hypothesis that each of the physiological coefficients in equations (1) to (3) is proportional to certain measured factors in the environment. Thus the photosynthetic coefficient is expressed by

$$P_h \backsimeq \frac{I_o}{7.7K}\,(1 - e^{-7.7K})\, N \,.\, e^{.069T} ,$$

[2] Previous studies of this type (Riley, 1946, 1947) have not utilized a photosynthetic temperature coefficient, but examination of broad, regional variations in the oxygen production of surface phytoplankton (Riley, Stommel and Bumpus, 1949) indicates that temperature is an important factor and ought to be included.

in which N is the nutrient effect described above; the other factors have already been specifically identified. The phytoplankton respiratory coefficient is assessed in terms of temperature,

$$R \backsimeq e^{.069T} ,$$

and it is reasonable to suppose that the grazing coefficient varies with the size of the zooplankton population Z:

$$G \backsimeq Z .$$

Therefore it should be possible with appropriate constants to combine all the factors into an equation that would express their net effect on the rate of phytoplankton growth. In developing these constants, there are the alternatives (a) to depend entirely on statistical fitting, or (b) to use the same constants that were developed in the theoretical analyses of other areas. The second alternative was chosen since it seemed to be of some interest to determine the degree of general applicability of physiological constants; however, it so happens that both methods lead to nearly the same results. Two corrections in the numerical values of constants were necessitated by differences in method. First, the inclusion of a temperature factor in photosynthesis must be allowed for. Thus the previous photosynthetic constant, with a numerical value of 2.5, was divided by the mean value of $e^{.069T}$, and the new value became 0.85. Second, zooplankton had been rated previously in terms of volume, and it now becomes necessary to express the factor as numbers of organisms. A statistical analysis of Kokubo's data on numbers of zooplankton and volume of total plankton was used to establish an average conversion factor.

Equation (3), rewritten in terms of environmental factors, can now be stated

$$ln \frac{P_t}{P_o} = \frac{0.85\, I_o}{7.7K} (I - e^{-7.7K})\, N.\, e^{.069T} - 0.0175e^{.069T} - 0.000136Z ,$$

in which the ratio $\frac{P_t}{P_o}$ represents the relative change in the population during a period of one day. On the basis of this equation it is now possible to construct a theoretical population curve by applying it to the observed numerical values of the various environmental factors, integrating successive short intervals (two-week periods) through the two years' observations. When this was done it was found that one additional factor must be taken into account. Instead of maintaining the same general level, the theoretical population at the end of

two years was much larger than it had been in the beginning. It was apparent that either the theoretical photosynthetic coefficient was too high, or some factor not properly accounted for was reducing the population. Statistical analyses indicated that the first alternative probably was not correct. Instead, realistic results were best obtained by subtracting a constant from the physiological terms, so that the equation became

$$ln \frac{P_t}{P_o} = \frac{0.85I_o}{7.7K}(1 - e^{-7.7K}) N.e^{.069T} - 0.0175e^{.069T} - 0.000136Z - 0.0393 . \quad (4)$$

Application of this equation yields relative population changes during the two-year period, and for comparison with the observed phytoplankton concentrations, the theoretical ratios can be converted to absolute concentrations by means of equation (2). The integration constant P_o is arbitrarily chosen. Hence, in the theoretical curve shown in Fig. 5, absolute concentrations have no fundamental meaning; it is only relative variations that are significant.

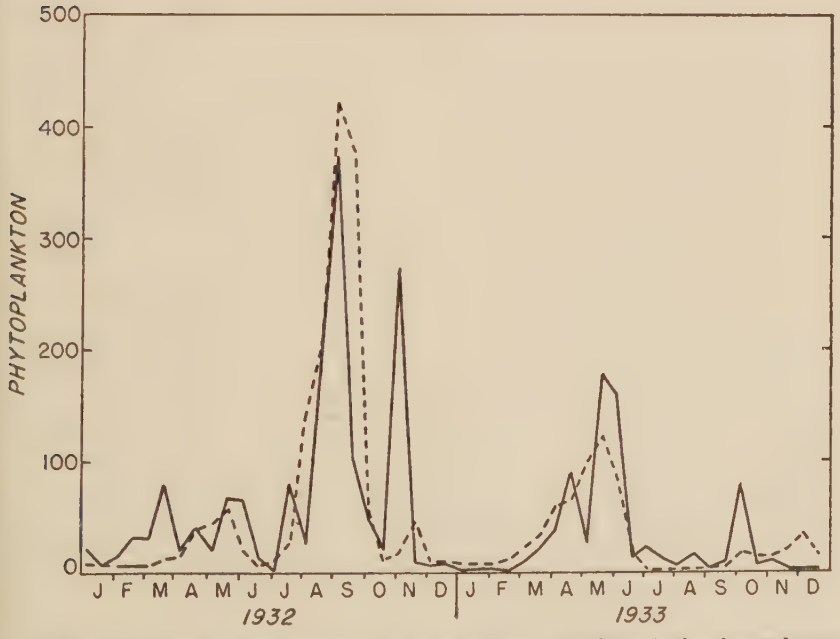

Figure 5. Phytoplankton, thousands of cells per liter. Solid line is the observed population. Broken line is a theoretical curve derived from environmental factors according to equations (2) and (4).

DISCUSSION

The agreement berween the observed and calculated populations in Fig. 5 is by no means perfect; however, it is apparent that the major objective has been accomplished, since the observed differences from one year to the next in the relative size of the populations and in the relative magnitude of individual flowerings are more or less preserved in the theoretical treatment. Therefore, by examining the environmental data step by step with respect to the way in which the component factors fit together in the equation, it becomes possible to discuss the environmental influences in the Husan area with a deeper insight into the principles of phytoplankton growth than would be possible simply by inspection of the primary data. The conclusions are summarized as follows:

The growth rate of the Husan plankton is higher, with any given complex of light, temperature, and nutrients, than in previous studies of other areas. This is indicated by the necessity of including a negative constant in the equation in order to make the cycle balance. There is a simple physical reason for this result. In shallow water, where the light intensity is adequate for growth from surface to bottom, the average growth rate is expected to be higher than in deeper water where some part of the population is always found below the compensation depth. The negative constant presumably means that the higher growth rate is balanced by a continual drain on the population by the outflow of water from Husan Harbor and by lateral mixing with the sparser populations of deeper water. It is an over-simplification of the facts to assume that such losses actually are constant, and undoubtedly better agreement could be obtained between observed and calculated populations if more were known about the hydrography of the region. The available data on the subject tend to support this contention. If the probable population loss is rated as the difference between theoretical and observed population changes during successive two-week periods, there is a small but significant correlation of the order of 0.2 between these values and the increase in the salinity of the water during the same periods. The salinity change is of course indicative, at least in part, of interchange with water of higher salinity off shore, but its value as a quantitative indicator of lateral mixing is considerably reduced by the fact that the salinity must also be affected by variations in the flow of river water into the harbor.

The seasonal fluctuation in the mean radiation in the water column is relatively smaller than that of incident radiation. This results from high transparency of the water in midwinter and lower values

in late spring and summer. Since these variations in transparency are correlated to a considerable degree with the size of the phytoplankton population, the latter can be said to behave in this respect as a self-regulating mechanism, reducing its growth rate as the population density increases and vice versa. Self-regulatory mechanisms probably also exist in the relations of phytoplankton with nutrients and zooplankton. Thus seasonal fluctuation in growth coefficients seem to be less than that of the basic physical factors.

Each major flowering is accompanied by nutrient depletion (phosphate, nitrate, or both), and this is the chief factor responsible for its termination. The length and severity of the depletion is correlated with the size of the preceding flowering and is also reflected in the extent of the population decline and the time required for the population to recover and produce the next flowering. The net result is that a large summer flowering tends to occur after a small spring one and vice versa.

While nutrients appear to be the most important factors to be considered in connection with summer flowerings, it is apparent that every other factor also contributed to produce the great difference between the summer-autumn flowerings of 1932 and 1933. In 1932 the nutrients recovered in late June, so that a flowering was possible any time thereafter, and during the next month the effective radiation was greater than it was during the analogous recovery period of 1933, which began in late July. During these periods of potential augmentation, the temperature and the quantity of zooplankton were less in 1932, so that there was less opportunity for the dissipation of organic matter by respiration and grazing.

During the period from late autumn to early spring, the adverse influences of the summer—nutrient depletion, respiration, grazing—were reduced to a minimum. As far as the theoretical analysis is concerned, the difference in the spring flowerings of 1932 and 1933 was the result of rather small differences in the magnitude and duration of the spring radiation pulses, and the midwinter minima were caused by low radiation at that season. Admittedly the theoretical curve is not a very good fit for this part of the data, and there must be important undescribed factors. In particular, it seems likely that the inshore population is very susceptible during the early stages of the spring flowering to losses by lateral mixing with offshore water, where presumably the flowering begins later.

SUMMARY

1. Published data on the plankton of Husan Harbor, Korea and its environmental factors during 1932 and 1933 are used as the basis

for a theoretical investigation of the reasons for differences that occur from one year to the next in phytoplankton seasonal cycles.

2. The analysis utilizes methods previously developed for the study of other regions, with a few slight modifications necessitated by local conditions and by differences in methods of measurement. A simple differential equation is written, in which the rate of change of the phytoplankton population is described in terms of physiological processes that increase or decrease its organic content (photosynthesis, respiration, and grazing), and in which the rates of the individual processes are quantitatively assessed by reference to a few environmental factors—radiation, transparency, temperature, phosphate, nitrate, and the quantity of zooplankton. Application of these factors to the equation results in a theoretical phytoplankton curve that is essentially in agreement with observed phytoplankton concentrations.

3. Nutrient salts appear to be the most important factors determining the time, duration, and relative magnitude of summer and autumn flowerings, although all the other factors have some influence. The midwinter minima and spring flowerings seem to be controlled primarily by radiation.

4. Marked differences in seasonal cycles from one year to the next are depicted with sufficient accuracy by the theoretical curves to leave little doubt that they are largely caused by variations in the factors listed.

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THE DISTRIBUTION OF THE EGGS OF *VAMPYROTEUTHIS INFERNALIS* CHUN[1]

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INTRODUCTION

Vampyroteuthis infernalis Chun is a bathypelagic dibranchiate cephalopod of such peculiar character, in some respects specialized and in some respects primitive, that it cannot be placed in either of the living suborders but appears to be more nearly akin to certain Mesozoic fossils. A preliminary account of the structure and relationships of this animal has been given (Pickford, 1940), a detailed study of the external anatomy and of the gladius is in press, and the internal anatomy is still under investigation. The natural history and distribution of *Vampyroteuthis* has also been examined (Pickford, 1946) and may be summarized briefly. *V. infernalis* occurs predominantly in the Deep Waters of tropical and subtropical oceans, the northern and southern limits corresponding roughly to the fortieth parallels of latitude. The vertical distribution ranges from 300 to 3,000 meters, with the majority at 1,500 to 2,000 meters. Hydrographic analysis indicates that the species is stenothermic, stenohaline and oligoaerobic. Nearly all specimens have been taken from regions in which the oxygen content of the water was upwardly decreasing, i. e. from just below the oxygen minimum. The water masses inhabited by the species have been analyzed by plotting the distribution on temperature-salinity charts. Dr. E. F. Thompson made the further important suggestion that it is neither temperature nor salinity that is the limiting factor, but rather the density resulting from a combination of the two. Thus Pacific specimens inhabit colder and less saline water than those from the Atlantic, although the density layer is the same.

DESCRIPTION

The ripe ovarian eggs of *Vampyroteuthis infernalis* are known from a single, gravid female taken by the Dana Expedition, 1928–30, in the

[1] Papers from the "Dana" Oceanographical Collections, No. 30.

Gulf of Panama (Pickford, 1946: table 1; specimen No. 1). Even in this specimen the majority of the eggs are still in various stages of formation, but 21 eggs are already provided with a well-formed capsule and the follicle sheath is either very thin and ready to be peeled away, or, in a few cases, has ruptured and been discarded. The animal had copulated, as evidenced by the presence of spermatophores in the spermatophore-receptacles, and was undoubtedly preparing to spawn.

TABLE I.—List of Eggs Attributed to *Vampyroteuthis infernalis*

Station	*No. Eggs*	*Diam. (mm.)*	*Micropyle*	*Observations*
1152 II	1	3.44	Present	Egg quite typical
1156 VI	1	3.86	Present, but difficult to see	Otherwise typical
1157 VI	1	3.95	Present	Egg quite typical
1171 X	1	3.53	Present	Egg quite typical
1217 II	1	3.95	Present	Egg quite typical
1242 XII	1	3.72	Present	Egg quite typical
1261 VII	1	3.91	Present	Egg quite typical
1267 IV	1	3.91	Present	Egg quite typical
1269 II	2	3.81, 4.00	Present	Eggs quite typical
1358 IV	1	3.91	Almost certainly present	Otherwise typical
1365 X	1	3.95	Present	Has early blastodisc
1365 XI	1	3.95	Present	Egg quite typical
3768 II	1	3.95	Present	Egg quite typical
3980 VIII	1	4.00	Present	Egg quite typical

The most perfectly preserved eggs are spherical; the diameters of three such eggs, free of the follicle sheath, are: 3.30, 3.35 and 3.35 mm. (average: 3.33 mm.). These measurements were made in neutral sea water formalin, in which the animal was preserved. If the eggs are transferred to distilled water they swell; the smallest of the three listed above increased from 3.30 to 3.43 mm. The color is a light yellowish-brown, and the egg is quite opaque, at least in the preserved condition, probably also in life. No large oil globules are present, although, under the high power of the binocular, many minute oil droplets as well as small aggregates of fine white material can be seen interspersed with the yolk. There is no perivitelline space; the egg capsule is quite thin and adheres closely to the ovum. The surface of the capsule is shiny and finely alutaceous. The micropyle is fairly conspicuous, not so much on account of its size, which is minute, but on account of the presence of a small area of glistening white material situated immediately beneath it, and also, in most cases, because of the presence of fine radiating lines that converge upon it from the surrounding surface of the capsule.

None of the above-described features can be considered as diagnostic, and it must be admitted that any one of them, and almost any combi-

nation of them, might be found in a fish egg or, perhaps, in the hitherto undescribed pelagic egg of some lesser known cephalopod. Furthermore, certain features, such as size and color, might be expected to vary considerably, and no doubt a space would appear between the capsule and the embryo during development. Nevertheless, in the absence of evidence to the contrary, it seems legitimate to assume that an egg taken from a bathypelagic haul in water known to be inhabited by *Vampyroteuthis*, and presenting all of the features outlined above, within reasonable limits of size and color variation, may safely be attributed to this species. It was decided, therefore, to survey the egg collections of the DANA Expeditions, with a view to finding whether such eggs were present.

At first all samples were examined, but it soon became evident that material collected with a towline of less than 1,000 meters never contained any eggs that even vaguely resembled those of *Vampyroteuthis*. This is entirely in accordance with the vertical distribution of the species, which never ascends so near to the surface. Subsequently attention was therefore concentrated on samples that had been taken with 1,000 meters wire or over. However, in order not to prejudice the argument, no attention was paid to geographical data.

A rapid preliminary sortation, without microscopic examination, yielded some 50 eggs, representing 44 different hauls, which resembled the eggs of *Vampyroteuthis* in a general manner. About half of these were rejected upon closer study, some even containing recognizable fish embryos upon the surface of the yolk. There remained just 23 eggs which could not be definitely rejected on obvious grounds; of these the 15 listed in Table I combine all the features of the *Vampyroteuthis* egg and may reasonably be attributed to this species. Eight others are recorded as doubtful, either because the micropyle could not be seen clearly, or for other reasons noted in Table II. Probably some of them really belong to *V. infernalis*, but it is equally possible that closely similar, yet distinctive, eggs do actually occur in the bathyplankton. The three eggs taken at St. 1365 XI provide an interesting confirmation of this point (cf. Tables I and II). One egg, attributed to *Vampyroteuthis*, is a little larger than the other two, 3.95 as against 3.65 mm. in diameter, although all three are well within the size-range of eggs definitely assigned to this species. However, the larger egg has a perfectly characteristic micropyle while this structure cannot be discovered on the other two by external examination. The two slightly smaller eggs also contain more conspicuous masses of white crystals. Thus it appears that two eggs, taken in the same haul with an indubitable egg of *Vampyroteuthis* and very closely similar to

TABLE II.—List of Eggs Doubtfully Attributable to *Vampyroteuthis infernalis*

Station	*No. Eggs*	*Diam. (mm.)*	*Micropyle*	*Observations*
1157 VII	1	3.53	Not definitely seen	Has early blastodisc
1165 VIII	1	3.26	Not seen	Probably not *V. i.* yolk more translucent. Has blastodisc.
1217 V	1	3.72	Present (?)	Has blastodisc
1269 V	1	3.63	Not seen	
1265 XI	2	3.63	Not seen	More white crystals than typical *V. i.* egg from same haul
3548 II	1	3.44	Not seen	Distorted, has narrow perivitelline space
3686 VIII	1	3.91	Not seen	Has blastodisc and perivitelline space
3736 II	1	3.72	Not definitely seen	Has blastodisc
4007 VIII	1	(?)	(?)	Poor condition, squashed, possibly *V. i.*

it except in the minutest details, must nevertheless be rejected as of doubtful character.

The features of the 15 accepted *Vampyroteuthis* eggs may now be discussed. It is at once noticed that the average size is somewhat larger than that of the ovarian eggs; the range is 3.44 − 4.00 mm., the average 3.86 ± 0.17 mm. This is probably to be expected, since it is very likely that the eggs swell slightly after they have been laid and may continue to do so during development. The eggs of certain Octopoda certainly increase in size during development. My attention was recently called to this point by Mrs. G. E. MacGinnity (*in litt.*) in connection with the eggs of a California species that were kept under observation in an aquarium. The *Vampyroteuthis* eggs of the plankton samples are almost pearly white in color, much paler than the ovarian eggs. This difference may be discounted. As pointed out by Dr. Å. Vedel Tåning (in litt.), and by Pickford (1946: p. 5) in the Dana Report on *Vampyroteuthis*, the neutral sea water formalin in which these specimens were preserved becomes deep purple in color with time, no doubt due to solution of the melanin, which probably contributes to the discoloration of the eggs. Moreover, color is likely not to be an important character; for example, eggs of the two Florida species, *Octopus joubini* Robson and *O. briareus* Robson, vary from pearly white to a deep golden brown. None of the 15 eggs possess any trace of a perivitelline space; this might become apparent in later developmental stages, but unfortunately only one egg contains a developing embryo and this is an early blastodisc. A few of the doubtful eggs have segmentation stages and some show a narrow perivitelline space. It was a great disappointment that no advanced embryos of *Vampyroteuthis* were discovered. Dr. Tåning suggests (in litt.) "that the eggs when developing sink to deeper water layers—this I have

experienced in several deep sea fishes—and you have accordingly not got them, because we have not fished sufficiently deep down." Evidence presented in the next section appears to militate against this interpretation, since both eggs and all stages, from larvae to adults, tend to be restricted to a rather limited density layer.

Some other observations by Dr. Tåning, who kindly examined the eggs, may also be quoted to round out the discussion. He states (in litt.) that "The eggs . . . are—as far as I can see—not fish eggs; their uniform appearance seems to indicate, that they are from the same species or related species; the depth in which they have been secured (about 500–2500 metres) is in accordance with your supposition that they are eggs of *Vampyroteuthis*. The micropyle may often be difficult to see in eggs and the general appearance of the doubtful eggs seems to indicate that they also belong to the same species." Furthermore, Dr. Tåning points out "that all preserved eggs—fish and others as well—will shrink rather much during the years; they are as you know preserved in 4% formalin and many of them during 20 years or more; probably they might have had a diameter about 20% larger than now, when fresh." But, as he also points out, this shrinkage must also affect the ovarian eggs.

In all other features, not noted above, the 15 selected and accepted eggs resemble the ovarian sample so closely as to be indistinguishable from it.

DISTRIBUTION

We may now turn to a consideration of seasonal, distributional and hydrographic data (Tables III–VIII). The 15 eggs represent only 13 stations, for two eggs were taken in one of the hauls (St. 1269 II), and St. 1365 is represented by two eggs from two different hauls. All of the stations are from regions known, or safely presumed, to be inhabited by *Vampyroteuthis*, and seven of the stations actually yielded specimens of this species, either from the same haul as the egg or from a parallel one at a somewhat different depth. Two stations are perhaps of special interest: St. 3980 in the South Atlantic is situated rather close to the southernmost Atlantic record for the species (specimen No. 50; Pickford, 1946). The latter, a VALDIVIA specimen, was taken in the Cape Basin, just south of the Walfisch Ridge, but the DANA egg was caught to the north of the ridge. The egg from St. 1171 is from the Guiana Basin, about midway between the well investigated and well populated waters adjacent to the West Indies and the Brazil Basin, where an isolated record was made by the ROSAURA. An egg was also taken from the St. Croix Basin (St. 1167 IV), from whence also one specimen is known, confirming the fact that the North

TABLE III.—Station Data for Accepted Eggs of *Vampyroteuthis infernalis*

Station	*Date*	*Latitude and Longitude*	*Ocean Basin*	*Bottom (meters)*	*Towline (meters)*	*Gear*	*Comments**
1152 II	22.X.1921	30° 17′ N. 20° 44′ W.	Canaries	—	5000	S150	
1156 VI	25.X.1921	25° 11′ N. 20° 57′ W.	Canaries	4000	5000	S150	Spec. No. 73 taken in this haul.
1157 VI	27.X.1921	21° 57′ N. 22° 58′ W.	Canaries	4800	4000	S150	
1171 X	13.XI.1921	8° 19′ N. 44° 35′ W.	Guiana	—	4000	S150	
1217 II	27.I.1922	18° 50′ N. 79° 07′ W.	E. Caribbean	—	3500	S100	Spec. No. 22 taken with 2,500 m.w., haul IV.
1242 XII	15.II.1922	24° 05′ N. 74° 36′ W.	N. American	3600	3500	S150	Spec. No. 38 taken with 2,500 m.w., haul XIV.
1261 VII	9.III.1922	19° 04′ N. 65° 43′ W.	N. American	5340	4000	S150	Spec. Nos. 44 and 59 (or 71) taken with 3,000 m.w., haul IX.
1267 IV	14.III.1922	17° 56′ N. 64° 50′ W.	St. Croix	—	3000	S150	Spec. No. 69 taken with 2,000 m.w., haul V.
1269 II	15.III.1922	17° 13′ N. 64° 58′ W.	E. Caribbean	4250	4000	S150	Spec. No. 37 taken with 3,000 m.w., haul III.
1358 IV	2.VI.1922	28° 15′ N. 56° 00′ W.	N. American	—	4000	S150	Spec. No. 71 (or 59) taken with 3,000 m.w., haul V.
1365 X	8.VI.1922	31° 47′ N. 41° 41′ W.	Canaries	3300	4500	S100	
1365 XI	8.VI.1922	31° 47′ N. 41° 41′ W.	Canaries†	3300	4000	S150	
3768 II	24.VII.1929	1° 20′ S. 138° 22′ E.	Philippines	3040	3500	S150	Spec. No. 14 was taken somewhat north of this, St. 3751 VII.
3980 VIII	17.II.1930	23° 26′ S. 3° 56′ E.	Angola	4025	4000	S150	Separated from Spec. No. 50 by the Walfisch Ridge.

* Spec. Nos. in this column refer to Pickford (1946: table 1)
† Close to the mid-Atlantic ridge.

Atlantic and Caribbean *Vampyroteuthis* populations are in free communication with each other.

All the eggs were taken with stramin nets, two with S100 and 13 with S150. Nearly all were captured by the 1921–22 cruise of the DANA, perhaps on account of the more extensive use of suitable nets in the greater depths by this expedition. There are, in fact, only two eggs certainly referable to *Vampyroteuthis* that were taken by the 1928–30 expedition and, unfortunately, only one of these is not from the Atlantic (St. 3768 II, Philippines Basin). Thus 14 of the 15 known eggs are from Atlantic waters.

TABLE IV.—VERTICAL DISTRIBUTION OF *Vampyroteuthis* EGGS

	Towline (meters)		
Ocean	*3,000–3,999*	*4,000–4,999*	*5,000–5,999*
Atlantic	3	9	2
Pacific	1	–	–
Total	4	9	2

The vertical *range* (Table IV) is concordant with the known depth distribution of the species and does not exceed it, either upwards or downwards. However, most of the eggs are from depths corresponding to 4,000–4,999 meters wire (2,000–2,500 meters), in striking contrast to the peak frequency of the animals themselves at 3,000–3,999 m.w. (1,500–2,000 meters). In the Atlantic, from which most of the eggs were taken, the peak frequency for specimens is even somewhat nearer to the surface, 2,000–2,999 m.w. (1,000–1,500 meters). This situation is clearly correlated with the fact, discussed below, that the eggs are more closely limited to a restricted density layer. A further possible correlation is that the oxygen supply is less deficient at slightly greater depths and it may be supposed that the developing eggs are less well adapted to oligoaerobic conditions than the animals themselves.

The question of proximity to the bottom also enters into the discussion of vertical distribution. Unfortunately only eight of the 13 stations have depth soundings, but it is clear that none of the eggs taken at these stations could possibly have been captured within 250 meters of the bottom, even if the calculation is based on two-thirds the length of the towline instead of the more usually accepted one-half. This confirms the view already advanced by the author that vampyromorph eggs are pelagic and are not attached to or deposited in the vicinity of the bottom.

The seasonal distribution of the eggs is also of interest. It will be recalled that, as far as the Atlantic is concerned, there is no evidence of a breeding season. Larvae occur about equally frequently at all

times of the year, and almost nothing is known regarding the occurrence of sexually mature individuals in this ocean (Pickford, 1946: table 7). The distribution of eggs is equally nonseasonal (Table V), although it happens that the one egg containing visible evidence of segmentation was taken in June. The single Pacific egg was taken in July, but no comparison can be made with the gravid Pacific female, captured in September, since she was found in the Gulf of Panama on the opposite side of the Pacific Ocean.

TABLE V.—Seasonal Distribution of *Vampyroteuthis* eggs

Ocean	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
Atlantic	1	2	4	—	—	3	—	—	—	3	1	—
Pacific	—	—	—	—	—	—	1	—	—	—	—	—
Total	1	2	4	—	—	3	1	—	—	3	1	—

TABLE VI.—Distribution of *Vampyroteuthis* Eggs in Relation to Hydrographical Conditions

Egg		*Hydrographic Conditions*					
Station	*Half-length Towline (meters)*	*Station*	*Depth (meters)*	*Temp. (° C.)*	*Salinity (‰)*	*Oxygen (ml/L)*	*Density (σt)*
1152 II	2500	1152	2500	3.24	34.96	4.94	27.85
1156 VI	2500	1156	2500	3.24	34.99	4.00	27.88
1157 VI	2000	1157	2000	3.69	35.01	4.50	27.85
1171 X	2000	1171	2000	3.66	34.93	4.64	27.79
1217 II	1750	1217	1500	4.20	34.96	5.10	27.75
			2000	4.11	34.99	5.50	27.79
1242 XII	1750	1242	1500	3.98	34.96	5.97	27.78
			2000	3.48	34.96	5.88	27.82
1261 VII	2000	1261	2000	3.43	34.97	6.02	27.85
1267 IV	1500	1269	1500	(4.17)	(34.96)	(4.71)	(27.75)
*1269 II	2000	1269	2000	4.07	34.96	4.59	27.76
1358 IV	2000	1356	2000	(3.70)	(35.00)	(6.23)	(27.84)
1365 X	2250	1365	2000	3.88	35.05	6.00	27.85
			2500	3.36	35.00	6.01	27.88
1365 XI	2000	1365	2000	3.88	35.05	6.00	27.85
†3768 II	1750	3756	1500	(3.08)	(34.61)	(2.37)	(27.59)
			2000	(2.32)	(34.64)	(2.54)	(27.68)
3980 VIII	2000	3980	2000	3.06	34.91	5.32	27.73

* Two eggs
† Pacific

Attention may now be concentrated on the hydrographic correlations (Table VI). For the sake of simplicity, conditions will be considered only at one-half the length of the towline; this treatment appears to be justified by the more extensive study of larvae and adults, in which conditions over a range of depths from one-third to two-thirds the length of the towline were considered (Pickford, 1946). As a result of this it was discovered that the hydrographic conditions associated with the distribution of *Vampyroteuthis* are adequately expressed on a

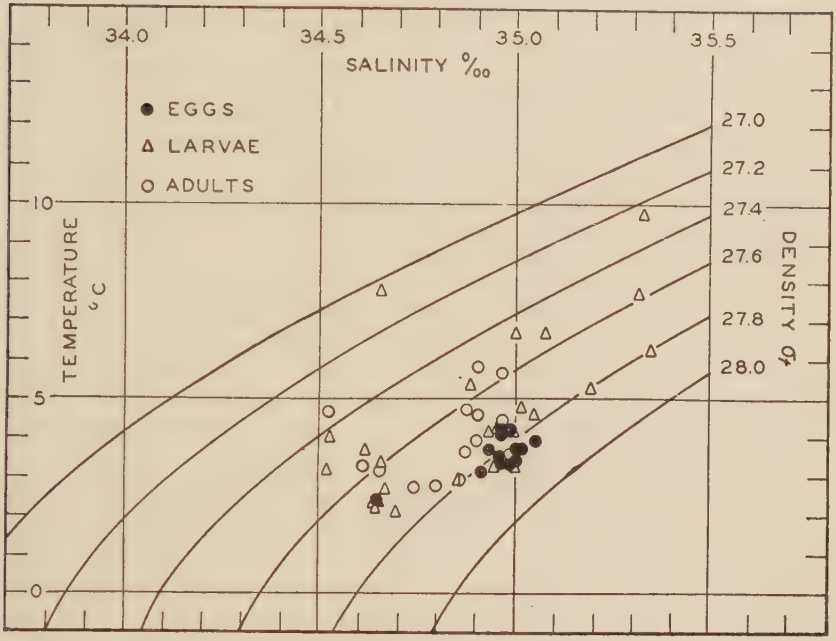

Figure 1. Distribution of eggs, larvae and adults (Stage-5) of *Vampyroteuthis* in relation to density layers of the ocean. Each point represents conditions at one-half the length of the towline, the most probable depth of capture.

temperature-salinity chart by a narrowly delimited density range at depths corresponding to half the length of the towline. The same conditions are strikingly true for the eggs (Fig. 1). The animals are found in waters of density ranging from σt 27.05 to 27.88, but the great majority occur between 27.40 and 27.80. A further analysis of the data (Table VII) shows that there is no difference in the density preferences of adults and larvae; however, there is a tendency for Atlantic specimens to spread into waters of slightly higher density. It is with these Atlantic specimens that the 14 Atlantic eggs must be compared (Table VIII). The extreme limits for the Atlantic eggs are 27.76–27.88, at temperature-salinity combinations suitable for the Deep Water of this ocean. From this it can be stated that the eggs are found in a narrowly restricted density layer that coincides with the bottom of the density range inhabited by larval and adult stages. Perhaps, after spawning, the eggs sink to this level if they are not already there and, as previously suggested, they thus benefit during development by the somewhat higher oxygen content of the deeper

TABLE VII. Distribution of Adults and Larvae of *Vampyroteuthis* in Respect to Density at One-half the Length of the Towline

Ocean	Density (σt)					Total
	27.00–27.19	27.20–27.39	27.40–27.59	27.60–27.79	27.80–27.89	
a. Adults						
Atlantic	—	—	—	2	3	5
Pacific	—	1	1	2	—	4
Indian	—	—	2	12	—	14
Total	—	1	3	16	3	23
b. Larvae						
Atlantic	—	1	5	6	6	18
Pacific	1	—	3	5	—	9
Indian	—	—	1	3	—	4
Total	1	1	9	14	6	31
c. All stages						
Atlantic	—	1	5	8	9	23
Pacific	1	1	4	7	—	13
Indian	—	—	3	15	—	18
Total	1	2	12	30	9	54

TABLE VIII. Distribution of Eggs of *Vampyroteuthis* in Respect to Density at One-half the Length of the Towline

Ocean	Density (σt)					Total
	27.00–27.19	27.20–27.39	27.40–27.59	27.60–27.99	27.80–27.99	
Atlantic	—	—	—	6	8	14
Pacific	—	—	1	—	—	1
Total	—	—	1	6	8	15

water. No Atlantic eggs were taken in water containing less than 4.00 ml/L, although the one Pacific egg might have been in water containing as little as 2.37 ml/L.

ACKNOWLEDGMENTS

I should like to express my thanks to Dr. Å. Vedel Tåning both for permission to study the egg collections of the Dana Expeditions and also for his most helpful suggestions and criticisms. My thanks are also due to the staff of the Marinbiologisk Laboratorium, especially to Miss Esther Hansen and Miss Eline Beck who worked with me in the laborious process of sorting the samples; to the many friends with whom I have discussed the problems, especially Dr. Anton F. Bruun; and to Dr. Daniel Merriman, Director of the Bingham Oceanographic Laboratory, for permission to pursue a part of my work in European laboratories.

SUMMARY

1. Fifteen bathypelagic eggs in the collections of the Dana Expeditions resemble the ovarian egg of *Vampyroteuthis infernalis* so closely

as to be attributed to this species. The average diameter is 3.86 ± 0.17 mm. as against 3.30 for ovarian eggs, but it is probable that the volume increases slightly after spawning.

2. Fourteen of the eggs are from the Atlantic and one is from the Philippines Basin; all are from regions known, or safely presumed, to be inhabited by *Vampyroteuthis.*

3. The eggs are found in slightly deeper water than the peak distribution of the animals themselves, but not outside the vertical range of the species.

4. The eggs are certainly pelagic; as far as is known none could have been taken within 250 meters of the bottom.

5. The occurrence of the eggs, like that of the larvae, is apparently nonseasonal.

6. The eggs occur in a layer of restricted density, in the Atlantic between σt 27.76 and 27.88, corresponding to the bottom of the density layer normally inhabited by the species.

7. Development is possibly favored by the greater amounts of dissolved oxygen in the deeper water, whereas the animals themselves are oligoaerobic and can range upwards under the roof of the oxygen minimum.

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THE FIELD USE OF A SALINITY-TEMPERATURE-DEPTH RECORDER[1]

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INTRODUCTION

A salinity-temperature-depth recorder that provides a continuous record of the salinity and temperature of sea water has been described by Jacobson.[2] The present paper is a discussion of the use of this instrument in the field and of its application to a variety of hydrographic problems.[3]

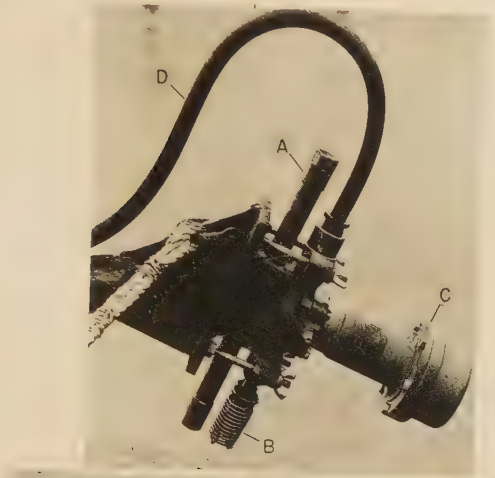
The instrument consists of a measuring unit connected to a computing and recording assembly by an appropriate length of multiple-lead cable. The measuring unit, shown in Fig. 1, responds to the temperature and conductivity of the sea water and to the pressure (depth) at which these variables are being measured. In the computing and recording assembly, shown in Fig. 2, the salinity is automatically computed from the conductivity and temperature signals and is recorded together with the temperature and the depth on a moving chart. The instrument operates on a 110-volt 60-cycle current. The salinity is determined over the range 20 to 40 °/₀₀, generally with an error not exceeding ±0.25 °/₀₀, and the temperatures from 28° to 90° F. are recorded with a limit of error of about ±0.2° F.

Several instruments have been built. The first was an experimen-

[1] Contribution No. 459 from the Woods Hole Oceanographic Institution. This paper is based in part on research conducted under contract with the Bureau of Ships, Navy Department, which has given its permission for publication. The instrument was developed by the Bristol Company under subcontract with the Woods Hole Oceanographic Institution.

[2] Jacobson, A. W. An instrument for recording continuously the salinity, temperature, and depth of sea water. Trans. (mon.) Amer. Inst. elect. Engrs., Vol. 67: 714–722, August 1948.

[3] The author wishes to acknowledge the contributions of the many persons who have been associated with this work, particularly Allyn C. Vine, who initiated its development, A. W. Jacobson and John L. Russell, both of the Bristol Company, who designed and built the instrument, and A. C. Redfield, who has supervised the work since its inception. John Holmes and Otis Hunt have been responsible for shipboard installation and maintenance and Carlyle Hayes has assisted in much of the field work.



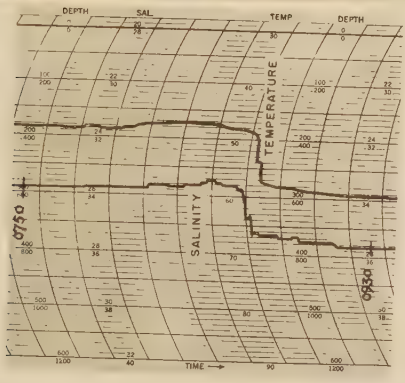


Figure 1 (top). Measuring unit mounted on outboard support. A, conductivity cell; B, resistance thermometer; C, depth element; D, cable. Figure 2 (middle). Recording unit, showing computer and strip chart at left, amplifier assembly at right. The dial in side of computer indicates conductance. Figure 3 (bottom). Record made while crossing northern boundary of Gulf Stream, April 24, 1947. Position at time 0750, 39°26' N, 69°55' W; at time 0930, 39°16' N, 69°52' W. Measuring element at 3.5 feet depth. Salinity scale 28-40 °/oo.

tal assembly which did not include a depth recording mechanism. Later models record depth and embody certain other improvements. Three of the instruments have each had several hundred hours of operation at sea.

For reasons of brevity and in view of the limited number of the models of the instrument, details on installation, testing and calibration are omitted. Such information may be obtained from either the Woods Hole Oceanographic Institution or the author.

APPLICATIONS

Field use of the instrument falls into two categories: (1) the determination of the horizontal distribution of salinity and temperature near the surface by continuous measurement from a moving vessel and (2) investigations of the vertical distribution of these variables during which the vessel must be hove to. In either case the instrument has proved useful, since it gives a continuous record of the variables and because the observer is immediately informed of existing conditions, thus permitting the survey program to be adapted to best advantage at the time.

For surface studies three methods have been employed: (1) a continuous record is made during a voyage which reveals critical conditions along the course; (2) the ship is sailed on a grid to give adequate coverage to an area; and (3) a particular band of isohalines is followed by a zigzag course which repeatedly crosses them. To obtain such records of salinity and temperature the measuring unit is usually mounted on a support extending from the deck of the vessel into the water.

For vertical measurements two methods have been used. In shallow, sheltered waters with sharp gradients, the measuring unit is lowered stepwise on a measured cable and provision is made for flushing of the conductivity cell by a pump. In deeper water the depth recording mechanism is employed and the measuring unit is lowered continuously. This is conveniently done by the use of a gypsy-head winch. Examples of these methods are discussed below.

1. *The Recording of Critical Changes of Salinity and Temperature During a Voyage.* During a voyage which may be conducted for other purposes, information on surface conditions is conveniently obtained by operating the instrument continuously, thus providing records of critical changes in surface salinity and temperature. Such data have demonstrated, for example, that the boundaries of water masses are frequently remarkably sharp. Fig. 3 is a record made while crossing the northern edge of the Gulf Stream. In this case

the chart was moving at such a speed that one division corresponds to 2,700 yards traversed by the ship. Thus it may be seen that the transition from slope water to Gulf Stream water took place in about 500 yards, during which salinity increased by 1.6 °/₀₀ and the temperature by 9° F.

2. *The Determination of Surface Distribution of Salinity and Temperature by Operating on a Grid.* Studies of the distribution of surface salinity and temperature in an area are made by travelling back and forth on a grid with the instrument giving a continuous record of the salinity and temperature. Two examples of this technique follow:

The surface distribution of salinity in Mount Hope Bay, obtained during the ebb tide, is shown in Fig. 4. The course taken by the vessel is indicated by the fine straight lines. In two hours a rectangular area measuring roughly 1½ x 2½ miles, or 6¾ square miles, was covered.

The surface salinity distribution in an area off New York as it was found on 24 April 1948 is shown in Fig. 5. In this survey an area of 700 square miles was covered in 24 hours even though interrupted by other hydrographic operations.

3. *The Determination of Surface Distribution of Salinity by Following Isohalines.* Another method for examining the surface distribution of salinity is to trace a band of isohalines by a zigzag course. This method was used successfully in a study of the distribution of Merrimack River effluent in Ipswich Bay. The results, illustrated in Fig. 6, were obtained in a period of three hours.

The procedure followed in this study will be discussed in some detail, since the technique is generally applicable. Fig. 6A is a working plot (somewhat simplified) of the vessel's course and of the salinities as taken from the record. The plot was kept up-to-date during the course of the survey so that the developing pattern was known. It will be seen that the outer circuit appeared not to be closed. This was due to errors in dead-reckoning navigation which had to be relied upon for a part of the circuit. When corrections based on fixes and fathometer data subsequently available were applied, the finished pattern shown in Fig. 6B was constructed.

A portion of the actual trace, taken during this study, is given in Fig. 7, since it illustrates the type of record obtained in surface studies. It includes all of the inner circuit shown in Fig. 6. In order that the data on the trace may be translated into their geographical frame of reference, the record is marked with the time at which the vessel passes a known position or changes course or speed. It is

also valuable to note on the record such events as the lowering of a bathythermograph or of the crossing of rifts in the water.

4. *Vertical Measurements of Salinity and Temperature.* The usual procedure of obtaining vertical measurements of salinity and temperature is to lower the measuring unit supported by its own cable

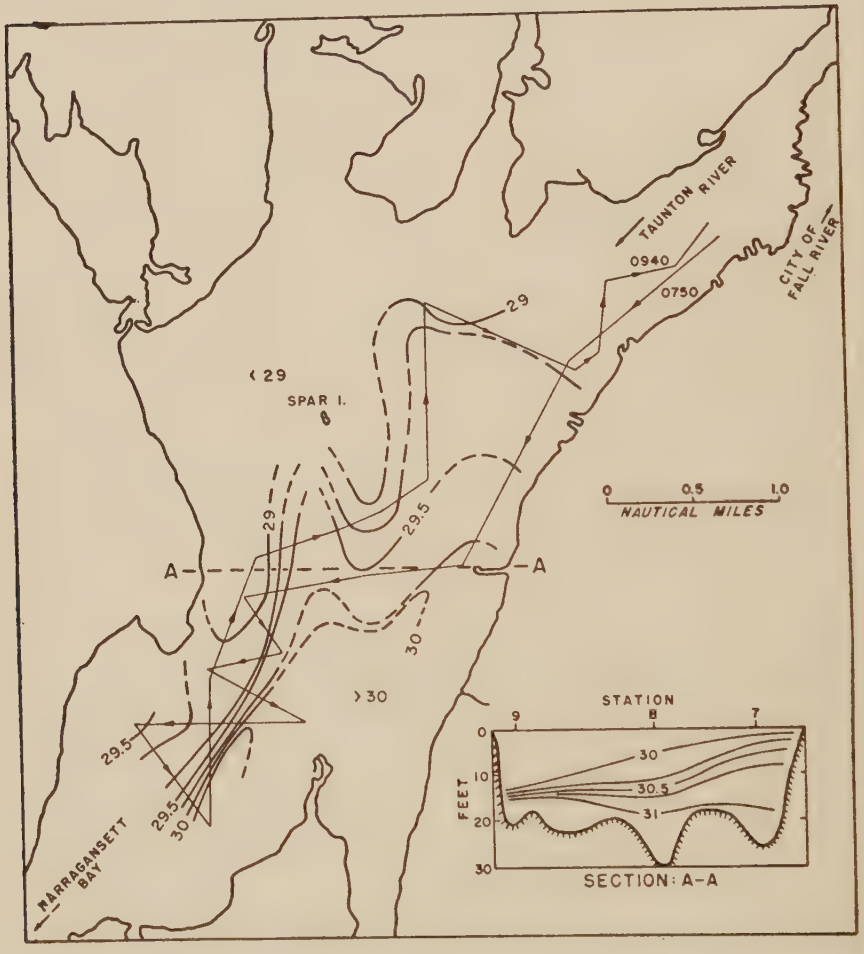


Figure 4. Distribution of salinity in surface waters of Mount Hope Bay. The light solid line shows course of vessel. Measuring element at 2.0 feet depth. November 10, 1944. Time 0750 to 0950.

Inset—Vertical section along A–A showing distribution of salinity in depth during ebb tide. November 13, 1945.

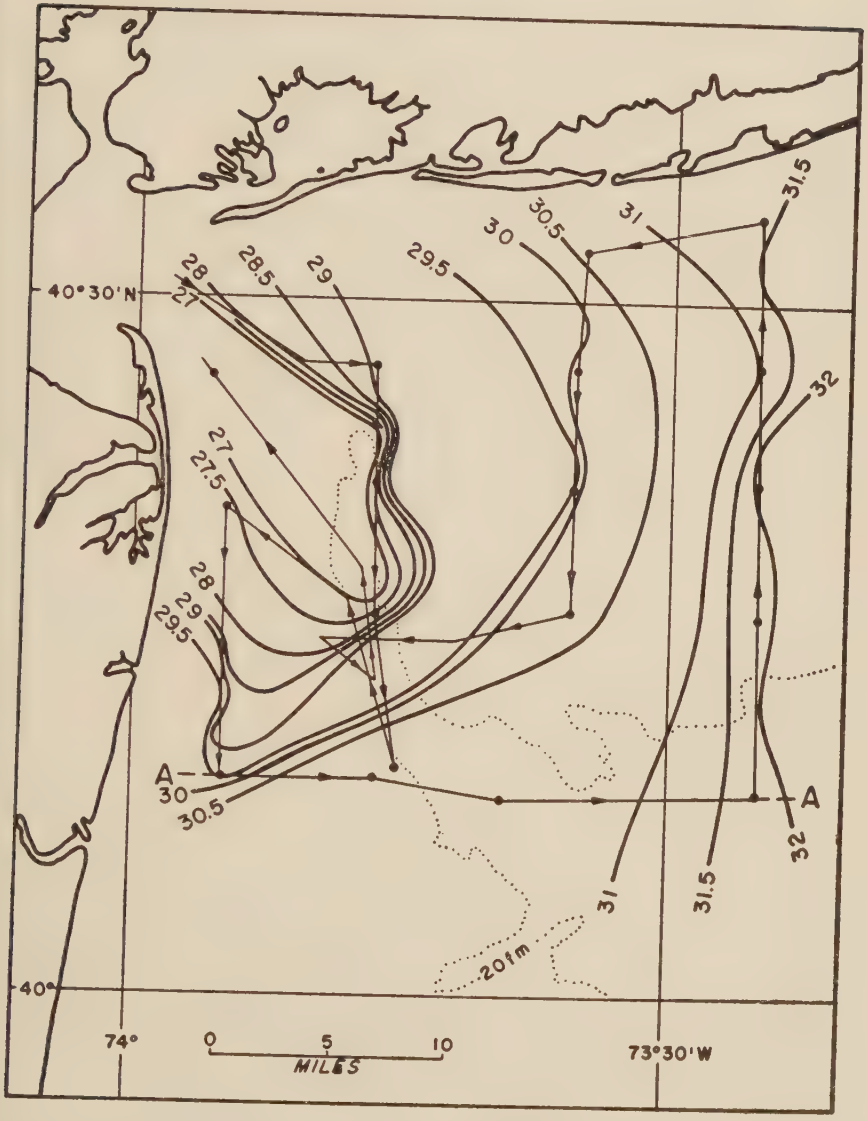


Figure 5. Distribution of salinity in surface waters off New York, April 24–25, 1948. Course of vessel shown by light line; isohalines by dark lines.

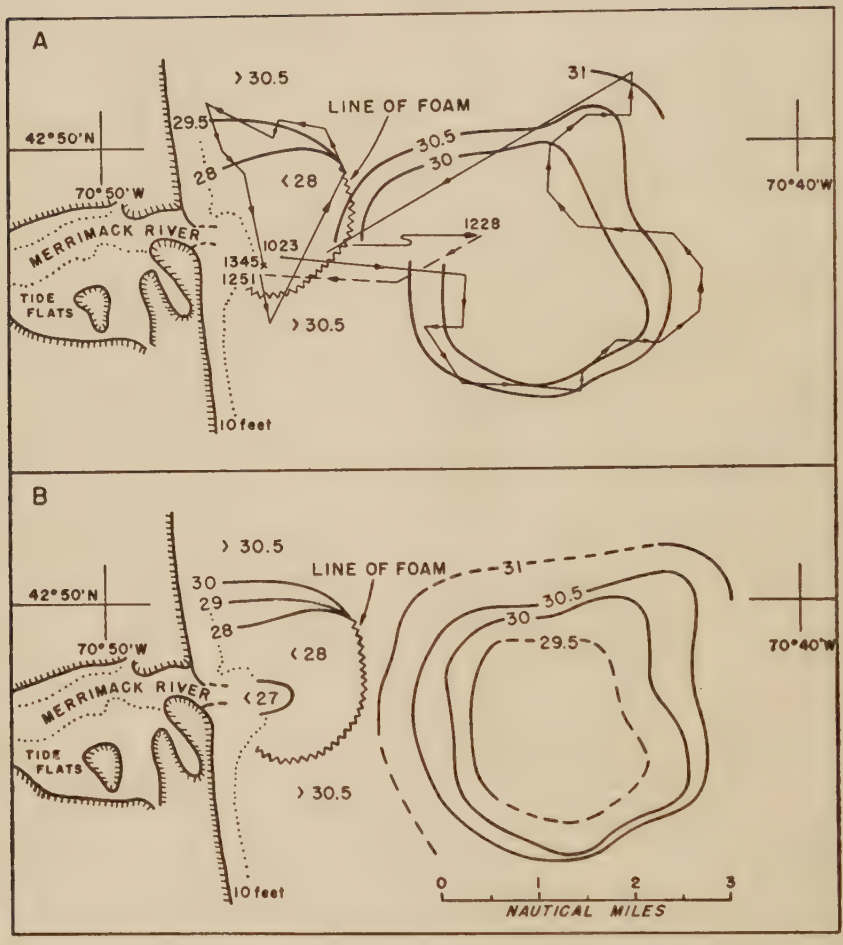


Figure 6. A. Working plot of distribution of isohalines at mouth of Merrimack River. The light line represents vessel's course by dead reckoning; the heavy lines show observed distribution of isohalines, the zigzag line shows position of foam at convergence of estuarine waters with the coastal water. September 7, 1946; time 1023 to 1345. High water was at 0934. Measuring element at 3 feet.

B. Reconstruction of distribution of salinity at mouth of Merrimack River after correcting for errors in dead reckoning. September 7, 1946.

while the vessel is hove to. If lowered at a rate of two to three feet per second, adequate flushing of the conductivity cell is ordinarily obtained. An example of the chart record that is obtained is given

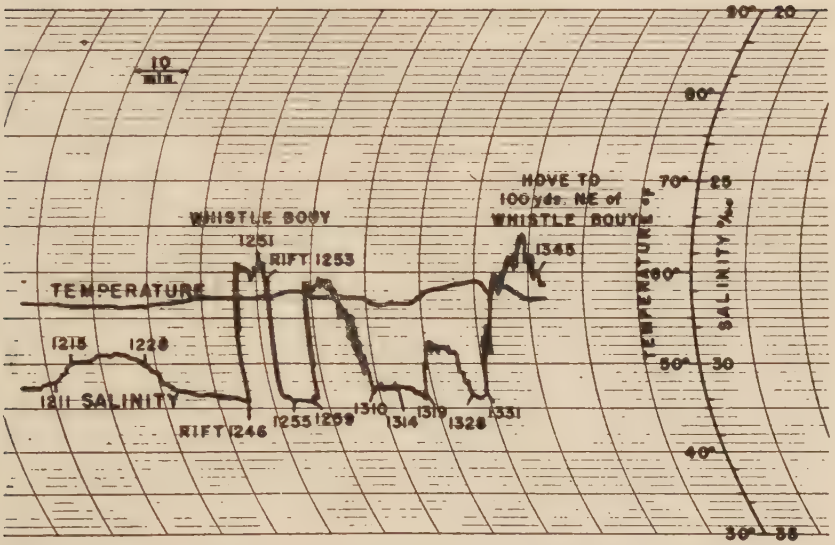


Figure 7. Record made during study of distribution of isohalines at mouth of Merrimack River, shown in Fig. 6. September 7, 1946; time 1200 to 1345.

in Fig. 8. On this occasion the lowering was completed in four minutes.

The jagged character of the depth trace is the result of the stepwise action of the depth-measuring mechanism, the unevenness of lowering by hand and of the roll of the vessel. The use of a gypsy-head winch improves the character of the depth trace.

Jogs appear in the salinity trace when abrupt temperature changes are encountered. One of these is identified at point A in Fig. 8 and corresponds to the temperature change at point B. Jogs originate in the fact that the automatic computation of salinity from temperature and conductivity assumes simultaneous measurement of these two variables, whereas in practice there is a tendency for the measurement of temperature to lag at points of abrupt change, hence introducing an error in salinity.

In Fig. 8 the arcs traversed by the three pens of the recorder are indicated as A, B and C. To read the record a transparent template, ruled with these arcs, is used.

To illustrate the accuracy that may be expected from the trace during a vertical lowering, the temperature and salinity from the record referred to above have been plotted as a function of depth in Fig. 9. Both the downward and upward traces are plotted to show the

combined effects of thermal lag in the resistance thermometer, "flushing" lag in the conductivity cell and sensitivity of the depth element. The latter has an error of about four feet. The combined effects, in this lowering, introduced an uncertainty of six to seven feet in the depth of the maximum gradient. The salinities, obtained by analysis of the

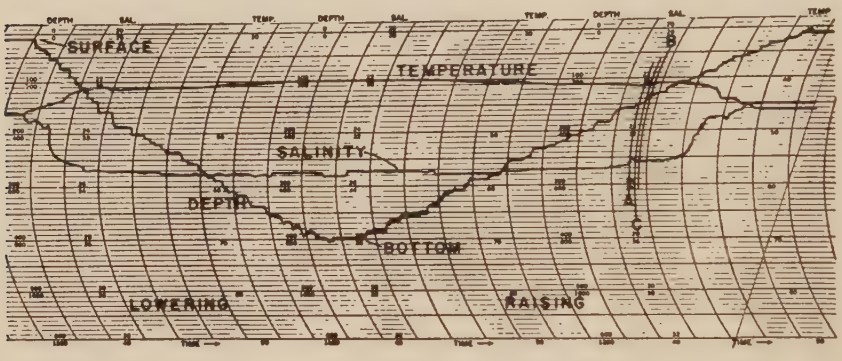


Figure 8. Record made during study of distribution of salinity and temperature with depth, off New York. Depth scale marked 100/200 equals 50 feet. Salinity scale 28–40 °/₀₀ in use.

Nansen bottle water sample using the Knudsen method, and the temperatures, as obtained from the reversing thermometers, have also been plotted in Fig. 9. The agreement with the recorded data is indicative of what can be expected of the instrument in routine operation.

In the course of determining the distribution of salinity off New York, lowerings were made on a grid work of stations (see Fig. 5) to establish its vertical distribution. A section from this grid is shown in Fig. 10 to illustrate the application of the instrument to the determination of salinity profiles. Of course temperature profiles, which are not shown, are also obtainable from the record.

In sheltered estuarine waters the vertical gradients of salinity and temperature are often very sharp and close to the surface, thus requiring accurate measurement of depth and a special procedure for avoiding the lag encountered when the measuring unit passes through the gradient. Since the depth recording mechanism provided with the instrument is not sufficiently accurate, depth is determined by measuring the amount of cable out. Lag is avoided by lowering the measuring unit stepwise, stopping at each depth long enough for equilibrium to be attained. Under these circumstances provision

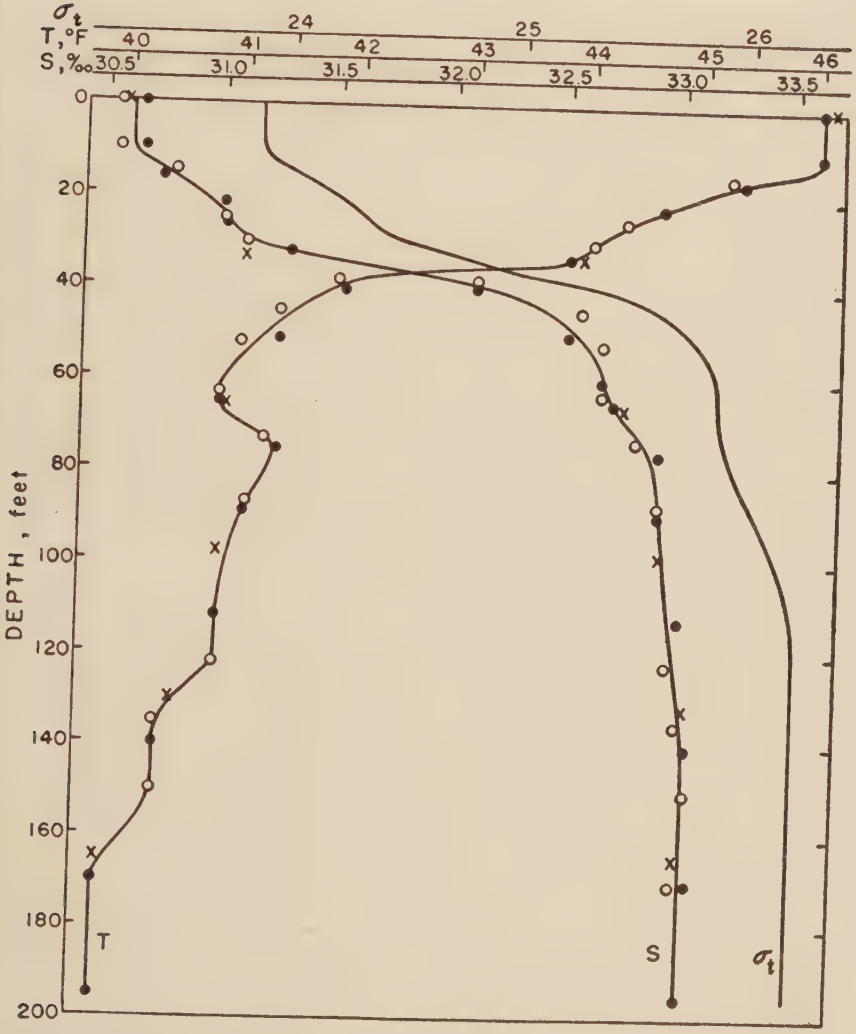


Figure 9. Plot of vertical distribution of salinity and temperature reconstructed from record shown in Fig. 8. The curves are drawn through points measured during lowering (dots) and raising (circles) of the measuring element after correcting for systematic errors of +0.5 ‰ in salinity and −0.2° F. in temperature. Crosses represent determinations made simultaneously by standard hydrographical procedures. The curve showing σ_t was obtained from the smoothed curves of temperature and salinity.

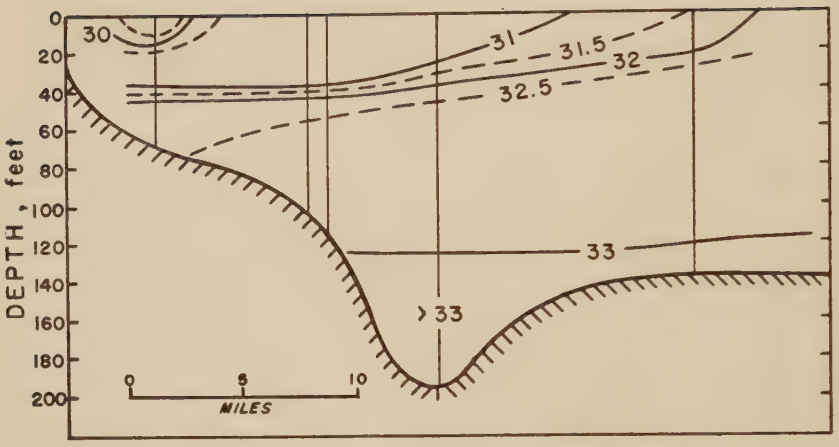


Figure 10. Vertical distribution of salinity along section A–A shown on Fig. 5 obtained by combining continuous observations of surface salinity and measurements made by lowering the measuring unit at the positions shown by light vertical lines.

must be made for flushing the conductivity cell. A small electric pump attached to the cell and powered through a cable from the vessel has proved satisfactory for this purpose. An example of results obtained by this procedure is given in the inset of Fig. 4.

Calibration. A constant check on the calibration must be maintained since it may vary with time. Therefore, water samples are taken at intervals during a survey and their salinity determined by the Knudsen method. The temperature is also checked with a suitable thermometer.

There are two types of error in the recording of both salinity and temperature, the systematic and inherent. Typical values of these errors, as determined during field operations, are given in Table I together with a definition of the terms. The systematic error is a function of the proper adjustment of the pen arm, various resistors in the circuit and the variable capacitors. Ideally, these may be adjusted to reduce the systematic error to zero, but in practice this is not feasible. The inherent error is the real uncertainty in the instrument's ability to measure the variable in question. It is a function of the temperature, salinity and design of the instrument.

TABLE I.—Examples of Systematic and Inherent Errors (in °/₀₀)

Cruise	S_0	S	a	k
Asterias	30.88	31.22	+0.34	+.21
7 Sept., 1946	30.91	31.20	+.29	+.16
	31.06	31.10	+.04	−.09
Temperature	31.13	31.35	+.22	+.09
53–55° F.	31.22	31.45	+.23	+.10
	31.16	31.27	+.13	.00
Recorder No. 0	31.00	30.95	−.05	−.18
	31.02	31.25	+.23	+.10
	31.08	31.23	+.15	+.02
	30.51	30.85	+.34	+.21
	30.95	30.80	−.15	−.27
	31.17	31.10	−.07	−.20
	31.14	31.25	+.11	−.02
	30.98	31.00	−.02	−.15
	30.90	31.00	+.10	−.03
	30.86	31.05	+.19	+.06
			$\bar{a}$ = +0.13	$\bar{k}$ = 0

Standard deviation = ±0.13
Spread = +0.21 to −0.27

Cruise	*Temp.*	S_0	S	a	k
Balanus B 9	47.0° F	32.68	32.20	−0.48	0.00
	56.7	34.45	33.97	−.48	.00
19–23 May, 1947	69.3	36.00	35.55	−.45	+.03
	75.5	36.07	35.75	−.32	+.16
Woods Hole to	77.0	36.18	35.65	−.53	−.05
Gulf Stream and	63.5	35.62	35.05	−.57	−.09
return	54.5	33.55	33.08	−.47	+.01
	50.0	32.92	32.25	−.67	−.19
Recorder No. 2	51.0	32.29	31.90	−.39	+.09
	54.0	31.85	31.40	−.45	+.03
				$\bar{a}$ = −0.48	$\bar{k}$ = 0.0

Standard deviation = ±0.10
Spread = +0.16 to −0.19

Note: S_0 = salinity by chemical analysis.
S = salinity by recorder.
$a = S - S_0$.
$\bar{a}$ = systematic error.
$k = a - \bar{a}$ = inherent error.

SUMMARY

Applications and operating characteristics of the salinity-temperature-depth recorder are demonstrated by illustrations taken from studies made on the effluent of the Merrimack River in Ipswich Bay, on the Taunton River-Mount Hope Bay estuary, on the waters off New York Harbor and on the Gulf Stream.

IODINE AND BROMINE IN SPONGES[1]

By

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and

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INTRODUCTION

Iodine and bromine have been known to occur in sponges since the early part of the nineteenth century. Since then a large number of analyses, primarily of the bath sponge but also of other sponges, have been reported. Both iodine and bromine have been found in most cases, although in greatly varying amounts. Even within the same species the discrepancies are great; thus Hundeshagen (5) found the iodine content of *Aplysina compressa* to be approximately 10%, while Ackermann and Burchard (1) concluded that it did not exceed 3%.

Mörner (7) has shown that in the Gorgoniaceae different families have different iodine-bromine ratios. Therefore it appeared of interest to ascertain whether any similar relationship also prevails in the Porifera. The iodine and bromine contents of a substantial number of species from Long Island, North Carolina, Florida, the Bahamas and Bermuda have been determined accordingly.

METHOD

1. The halogen content of the sponges from Long Island Sound was determined according to the method of Leipert as described by Ackermann and Müller (2).

2. The bromine and iodine contents of all other sponges were determined as follows: The sponges were oxidized with potassium permanganate in dilute sulfuric acid. Iodine was thereby oxidized to iodate, which remained in the flask. It was determined essentially according to the method of Groàk (4). Bromine was distilled out, absorbed by sodium hydroxide and determined by the method of Leipert and Watzlawek (6).

In a typical experiment, from 0.01 to 0.5 g. of powdered, air-dried sponge was placed in a 125 cc. standard taper Erlenmeyer flask with

[1] Contribution to the Study of Marine Products. XXII.

2 to 5 g. potassium permanganate and 15 to 25 cc. of 18N sulfuric acid. A standard taper joint, to which a bent tube had been sealed, was attached to the flask and the end of the tube dipped into a test-tube containing 10 cc. of 2N sodium hydroxide. The flask was then placed on a hot plate and heated until no more bubbles appeared in the sodium hydroxide (one to two hours). The tube was then detached and the flask cooled. The sodium hydroxide solution was transferred to an Erlenmeyer flask and bromine was determined according to the method of Leipert and Watzlawek (6). The material in the flask was diluted with water, the excess potassium permanganate destroyed with sodium nitrite and the excess nitrite decomposed with urea. After addition of potassium iodide the solution was titrated with 0.01N sodium thiosulfate.

DISCUSSION

In Table I the sponges are listed according to the classification of de Laubenfels (3); their iodine and bromine contents are given for the original material, for the organic matter and for the sponge less the foreign matter. Since it is almost impossible to wash sponges free of sand and shell fragments, the spicules and total ash were determined.[2] Except in the case of *Leucetta*, the ash other than spicules can be regarded as foreign matter. All foreign matter of the sponges collected in the Bahamas and in Bermuda, and some of the ash of the sponges from Florida and the northern Atlantic waters, is calcareous and dissolved during the acid oxidation process. It is therefore impossible to determine the ash and halogen contents on the same sample, and since even a small shell fragment can affect the analyses appreciably, the results must be regarded as approximate only. The error due to the loss of carbon dioxide from calcium carbonate during the ashing is quite small. Experiments with pure calcium carbonate have shown that, even with the most drastic ashing procedures, the loss is not more than 10%. A further inaccuracy is introduced by the air-drying of sponges, since some of the bromine of sea water remains on the sponge and is determined along with the sponge bromine; the amount is extremely small and can affect the value only in the second decimal place, except for the soluble proteins where the ash consists entirely of salt. The error due to iodine in sea water is negligible.

No detailed relationships between the halogen content of the sponges and their classification appear to exist. There are wide variations within the same genus, and even sponges of one species, collected at different times or in different localities, do not give constant results. Since it is believed that iodine and bromine are present exclusively in

[2] Data to be reported by Werner Bergmann in J. Mar. Res., *8* (2).

TABLE I. Bromine and Iodine Contents of Sponges

Sponge	Locality	Total Sponge (%)		Sponge, less extraneous matter (%)		Organic (%)		I/Br (% by wt.)	Atoms Br per atom I
		I	*Br*	*I*	*Br*	*I*	*Br*		
Class Demospongiae Order Keratosa									
Spongia obliqua skeleton	Bahamas	0.59	1.40	0.76	1.82	0.76	1.82	0.42	3.8
Spongia obliqua soluble protein	Bahamas	0.14	0.07	0.18	0.09	0.18	0.09	2.0	0.8
Bath Sponge	Commercial	1.21	2.66	1.21	2.66	1.21	2.66	0.45	3.5
Oligoceras hemorrhages	Bahamas	0.12	0.11	0.38	0.29	0.38	0.29	1.1	1.5
Hircinia variabilis skeleton	Bermuda	0.35	0.17	0.50	0.24	0.50	0.24	2.1	0.8
Hircinia variabilis soluble protein	Bermuda	0.07	0.82	0.10	1.12	0.10	1.12	0.09	18.6
Hircinia campana	Florida	0.61	0.98	1.24	2.00	1.24	2.00	0.62	2.6
Verongia fulva	Florida	0.16	1.46	0.16	1.46	0.16	1.46	0.11	14.5
Verongia fistularis	Bermuda	0.17	0.54	0.22	0.71	0.22	0.71	0.31	5.0
Dysidea crawshayi	Bermuda (Walsingham)	0.13	0.34	0.18	0.49	0.18	0.49	0.38	4.2
Dysidea crawshayi	Bermuda (Harington Sd.)	0.10	0.11	0.14	0.16	0.14	0.16	0.91	1.7
Dysidea etheria	Bermuda	0.27	0.38	0.35	0.49	0.35	0.49	0.71	2.2
Dysidea etheria	Bahamas	0.15	0.19	0.60	0.76	0.60	0.76	0.79	2.0
Ianthella sp.*	Bermuda	0.10	0.28	0.12	0.35	0.12	0.35	0.36	4.5
Order Haplosclerina									
Haliclona rubens	Florida	0.21	0.20	0.24	0.24	0.30	0.30	1.0	1.5
Haliclona viridis	Bermuda	0.17	0.05	0.19	0.06	0.27	0.08	3.4	0.5
Haliclona longleyi	Florida	0.13	0.17	0.13	0.17	0.24	0.31	0.76	2.1
Haliclona permollis	Bermuda	0.14	0.06	0.17	0.08	0.22	0.10	2.3	0.7
Haliclona permollis	L. I. Sound	0.16	0.09	0.17	0.10	0.29	0.16	1.8	0.9
Haliclona coerulescens	Florida	0.33	0.24	0.47	0.34	0.51	0.37	1.4	0.7
Haliclona oculata	L. I. Sound	0.24	0.19	0.25	0.20	0.37	0.29	1.3	1.3
Haliclona sp.*	Bermuda	0.46	0.31	0.60	0.40	0.66	0.44	1.5	1.1
Fibulia massa	Florida, 1945	0.20	0.08	—	—	—	—	2.5	0.6
Fibulia massa	Florida, 1948	0.07	0.27	0.23	0.87	0.35	1.35	0.26	6.1
Strongylacidon sp.*	Bermuda	0.28	0.58	0.42	0.88	0.61	1.25	0.48	3.3
Callyspongia vaginalis	Florida	0.33	0.18	0.44	0.24	0.44	0.24	1.8	0.9
Callyspongia vaginalis	Bermuda	0.17	0.21	0.22	0.28	0.22	0.28	0.81	2.0
Callyspongia fallax	Florida	0.55	0.28	—	—	—	—	2.0	0.8

* Species to be described by M. W. de Laubenfels

TABLE I. Bromine and Iodine Contents of Sponges (Cont.)

Sponge	Locality	Total Sponge (%)		Sponge, less extraneous matter (%)		Organic (%)		I/Br (% by wt.)	Atoms Br per atom I
		I	Br	I	Br	I	Br		
Order Poecilosclerina									
Pellina carbonaria	Florida	0.28	0.13	0.35	0.16	0.44	0.21	2.2	0.7
Rhizochalina hondurasensis	Florida	0.24	0.36	—	—	—	—	0.67	2.4
**Tedania ignis*	Bermuda	0.09	0.35	0.12	0.47	0.16	0.64	0.36	6.2
**Lissodendoryx isodictyalis*	Bermuda	0.10	0.16	0.14	0.22	0.16	0.25	0.63	2.5
Thalyseuripon sp.	Florida	0.27	0.09	—	—	—	—	3.0	0.5
Microciona prolifera	L. I. Sound	0.29	0.67	—	—	0.53	1.20	0.43	3.7
Order Halichondrina									
Axinella sp.†	Bermuda	0.04	0.03	0.05	0.04	0.06	0.05	1.3	1.2
Homaxinella sp.†	Bermuda	0.13	0.15	0.16	0.20	0.22	0.25	0.86	1.8
**Halichondria panicea*	L. I. Sound	0.06	0.07	0.10	0.11	0.24	0.28	0.86	1.9
**Halichrondria melanodocia*	Bahamas	0.07	0.18	0.09	0.22	0.15	0.38	0.39	4.1
Hymeniacidon heliophila	Beaufort	0.16	0.09	0.19	0.10	0.48	0.27	0.18	0.9
Order Hadromerina									
Spheciospongia sp.†	Bermuda	0.17	0.09	0.19	0.10	0.34	0.18	1.9	0.8
Suberites distortus	Florida	0.33	0.28	0.39	0.33	0.95	0.80	1.2	1.3
Suberites compacta	L. I. Sound	0.15	0.00	0.16	0.00	0.75	0.00	—	—
Aaptos sp.†	Bermuda	0.10	1.13	0.12	0.15	0.14	0.18	0.77	2.1
Terpios fujax	Bermuda	0.10	0.18	0.11	0.20	0.13	0.23	0.56	2.9
Placospongia melobesiodes	Florida	0.08	0.33	—	—	—	—	0.24	6.6
Cliona carriboea	Florida, 1940	0.12	0.04	—	—	0.46	0.15	3.0	0.5
Cliona carriboea	Florida, 1945	0.13	0.08	—	—	—	—	1.6	1.0
Cliona carriboea	Bermuda	0.08	0.10	0.14	0.18	0.17	0.21	0.80	2.0
Cliona celata	L. I. Sound	0.13	0.10	0.18	0.14	0.48	0.37	1.3	1.2
Order Epipoplasida									
Tethia sp.†	Bermuda	0.06	0.23	—	—	—	—	0.26	6.1
Order Choristida									
**Geodia gibberosa*	Florida	0.19	0.83	0.19	0.83	0.53	2.30	0.23	7.0
**Cynachyra cavernosa*	Bermuda	0.08	0.06	0.08	0.06	0.15	0.11	1.3	1.2
**Craniella crania*	Beaufort	0.18	0.06	0.20	0.08	0.49	0.16	3.0	0.5
Order Carnosa									
**Condrilla nucula*	Bermuda	0.05	0.10	0.07	0.13	0.07	0.13	0.50	3.2
Class Calcispongiae Order Asonosa									
Leucetta sp.†	Bermuda	0.19	0.06	—	—	0.35	0.11	3.2	0.5

* nonkeratinous without spongin.

† Species to be described by M. W. de Laubenfels.

the protein fraction of the sponge, their percentages in the organic fraction are calculated, but there again the differences within a genus or species are considerable. The most striking feature of the analyses is the sporadic distribution of the occurrence of high halogen contents. From Hundeshagen's (5) and Ackermann's (1) results one would conclude that sponges contain substantial amounts of iodine and bromine. This actually seems to be the exception rather than the rule. The author has found iodine and bromine values above 0.5% to be rare. It was not possible to duplicate Ackermann's results, except in the case of one commerical bath sponge where the author found 1.21% iodine and 2.93% bromine; Ackermann, in a West Indian bath sponge, found 1.41% iodine and 2.93% bromine. The species of both these sponges is unknown. In another bath sponge, *Spongia obliqua*, collected in the Bahamas, 0.54% iodine and 1.25% bromine were found. The extremely high halogen contents reported by Hundeshagen have never been duplicated and their value is doubtful, especially since no detailed method of analysis has ever been published.

The data do suggest, however, that the relationship of bromine and iodine may differ somewhat in the horny and the nonkeratinous sponges. Not only are the mean values rather different,

	I	Br
keratinous*	0.49	0.95 per cent of organic matter
nonkeratinous	0.35	0.40 per cent of organic matter,

*Excluding nonskeletal soluble proteins.

but it is evident that the keratinous sponges tend to contain more bromine relative to iodine than do the others. The differences are not due to selection by excluding samples without organic analyses, for the molecular ratio I/Br is found to be 3.9 for the keratinous and 2.1 for the nonkeratinous sponges, when all data, whether accompanied by organic analyses or not, are used. The ratio will be seen to be highly variable, but when the mean of the logarithms is compared by Fischer's t-test, which is the appropriate significance test in this case, the probability of the log. ratios being derived from the same array lies between 0.01 and 0.02, so that it is not unlikely that the difference is real. Examination of the data can be carried out also by means of correlation technique, which again suggests differences in the relationship of iodine and bromine when the two groups are compared. For the keratinous sponges for which organic analyses were carried out, the correlation coefficient of bromine on iodine is 0.713 which is highly significant ($P < 0.01$) even with only 12 pairs of observations; for the much greater series of nonkeratinous sponges the correlation coefficient

is 0.300, which is barely significant (P = 0.05–0.1) with 34 pairs of observations. Halogen accumulation seems to occur whether spongin is present or not. A striking example is *Geodia gibberosa* which lacks spongin but which contains 2.30% bromine when related to the organic matter. The data below are based on the per cent of iodine and bromine in the organic matter.

	I	Br
nonkeratinous with spongin	0.06–0.95 mean 0.37	0.00–1.20 mean 0.36
nonkeratinous without spongin (marked in Table I by *)	0.07–0.53 mean 0.24	0.11–2.30 mean 0.53

Also, there may be some geographical phenomenon underlying the observed variations. The histograms of Fig. 1 show the bromine and iodine contents of sponges calculated on the basis of the organic matter and arranged according to geographic location. It is of interest to note that more sponges from Florida and the Bahamas (Bimini) than from Bermuda show high bromine, and to a less extent high iodine, contents. Since about the same number of keratinous sponges were obtained from both localities and since there is no hydrographic reason for suspecting a difference in the composition of sea water in these regions, it appears possible that some difference in growth rate may be involved. It is at least reasonable to suppose that slow protein synthesis would give a greater opportunity for halogenation than fast formation.

The iodine-bromine ratios vary from 0.09 to 3.4 on a weight basis, with an average value of one. Since sea water contains about one thousand times more bromine than iodine, sponges concentrate iodine to a much larger extent than bromine. About 80% (or 0.4 mg. per liter) of the iodine in sea water is iodate (9); so far bromine has been reported entirely as bromide (8). An attempt was made to estimate bromate in sea water in the following manner: Atlantic water from off Woods Hole was concentrated and titrated with sodium thiosulfate after acidification and addition of potassium iodide and starch. The amount of thiosulfate calculated as needed for iodate was subtracted (about 1 cc. of 0.01N per liter) and the remainder was assumed to be due to bromate. An average of 1.5 cc. of 0.01N thiosulfate was needed, corresponding to about 0.4 mg. of bromate per liter. This figure merely indicates that the bromate concentration may be of the same order of magnitude as that of iodate, though the amount is so small that its significance may be doubted. Thus, while 80% of the iodine is iodate, not more than 0.6% of the bromine is present as bromate. Although it is not known in what form sponges take up hal-

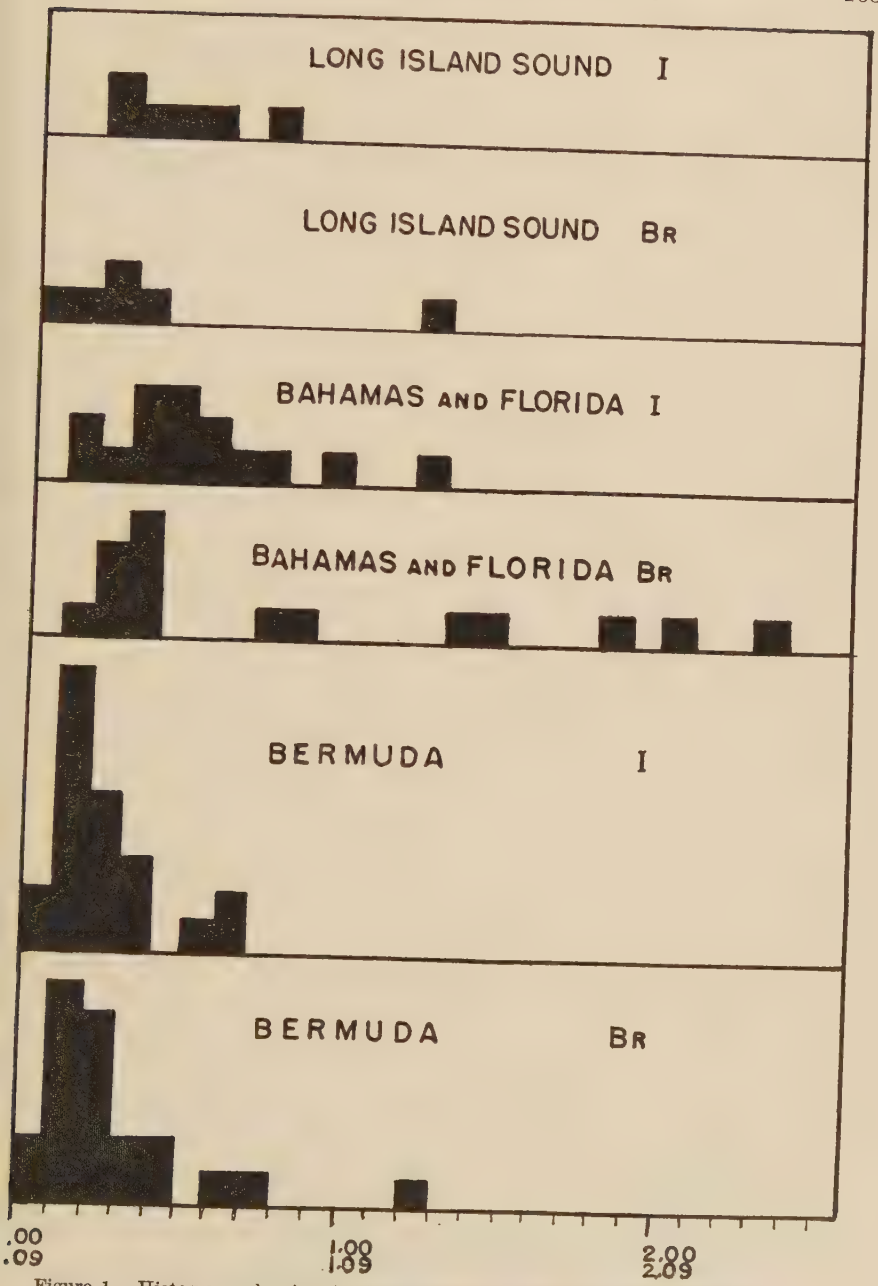

Figure 1. Histograms showing the distribution of bromine and iodine contents of the organic matter of sponges from various localities.

ogens, future work may show the presence of the ions of oxy-acids to be a significant factor in the mechanism of concentration.

The author wishes to express her gratitude to Werner Bergmann and Willard Hartman for collecting the sponges, to the Bermuda Biological Station, the Marine Biological Station of the University of Miami, the Lerner Marine Laboratory on Bimini and the Fisheries Laboratories at Beaufort for their assistance, and to Max W. de Laubenfels for classifying the sponges.

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SUMMARY

The keratinous sponges were found to contain from 0.12 to 1.21% iodine (average 0.48) and from 0.16 to 2.66% bromine (average 0.96). The nonkeratinous sponges were found to contain from 0.05 to 0.60% iodine (average 0.21) and from 0.00 to 0.88% bromine (average 0.24). The molecular ratio of iodine to bromine is 3.9 for the keratinous and 2.1 for the nonkeratinous sponges. On a weight basis the ratio was found to be one, averaging all results.

Only a few sponges, namely the bath sponge, *Hircinia campana* and *Verongia fulva*, contain more than 1% of iodine or bromine when calculated for the sponge less the extraneous matter.

It is believed that the keratinous sponges tend to have a greater I/Br ratio than the nonkeratinous sponges. There is also a possibility that the sponges from the Florida and Bimini areas contain more bromine and iodine than the sponges from Bermuda.

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